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THESIS

ESTIMATING THE DISTRIBUTION AND PRODUCTION OF MICROPLANKTON IN A COASTAL UPWELLING FRONT FROM THE CELLULAR CONTENT OF GUANOSINE-5' -TRIPHOSPHATE AND ADENOSINE-5'-TRIPHOSPHATE

by

Carol Diane Jori

September 1981

Thesis Advisor: Dr. E. D. Traganza

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REPORT DOCUMENTATION PAGE

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BEFORE COMPLETING FORM

1. REPORT NUMBER

2. GOVT ACCESSION NO.

3. RECIPIENT'S CATALOG NUMBER

4. TITLE (and Subtitle)
Estimating the Distribution and Production of Microplankton in a Coastal Upwelling Front from the Cellular Content of Guanosine-5'-Triphosphate and Adenosine-5'-Triphosphate

5. TYPE OF REPORT & PERIOD COVERED
Master's Thesis
September 1981

6. PERFORMING ORG. REPORT NUMBER

7. AUTHOR(s)
Carol Diane Jori

8. CONTRACT OR GRANT NUMBER(s)

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Naval Postgraduate School
Monterey, California 93940

10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS

11. CONTROLLING OFFICE NAME AND ADDRESS
Naval Postgraduate School
Monterey, California 93940

12. REPORT DATE

13. NUMBER OF PAGES
123

14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)

15. SECURITY CLASS. (of this report)
Unclassified

15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)
Approved for public release; distribution unlimited

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)
guanosine triphosphate, GTP
adenosine triphosphate, ATP
upwelling
productivity
biomass

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

This thesis examines the distribution and production of micro-organisms within a coastal upwelling front located off Pt. Sur, California. Underway measurements of adenosine-5'-triphosphate (ATP) and pigment fluorescence (principally chlorophyll a) were used to estimate the amount of living biomass present at 2.5 m. Specific and absolute productivity were measured by the nucleotide ratio of guanosine-5'-

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Estimating the Distribution and Production of Microplankton in a Coastal Upwelling Front from the Cellular Content of Guanosine-5'-Triphosphate and Adenosine-5'-Triphosphate

by

Carol Diane Jori
Lieutenant, United States Navy
B.S., University of Maryland, 1973

Submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE IN METEOROLOGY
AND OCEANOGRAPHY

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triphosphate (GTP) to ATP and GTP, respectively. This investigation was conducted to determine the significance and applicability of these productivity indices in studying the relationship of production and distribution of microplankton (principally algae) to frontal features in the coastal upwelling zone. The highest concentration of biomass associated with the highest rate of absolute productivity was preferentially located in the strong thermo-nutrient gradient in the warmer stratified water at the equatorward edge of the feature.

The measurement of specific productivity using the GTP to ATP ratio was significantly correlated with assimilation numbers (productivity index), lending support to the hypothesis that this ratio is a good indicator of specific community productivity in microplankton (principally phytoplankton).

No correlation existed between the GTP concentration which was enzymatically determined, and the concentration of GTP which was inferred from the calculated values of Δ ATP. This finding indicates that Δ ATP is not a good estimator of GTP in community assemblages of microplankton.

ABSTRACT

This thesis examines the distribution and production of micro-organisms within a coastal upwelling front located off Pt. Sur, California. Underway measurements of adenosine-5'-triphosphate (ATP) and pigment fluorescence (principally chlorophyll a) were used to estimate the amount of living biomass present at 2.5 m. Specific and absolute productivity were measured by the nucleotide ratio of guanosine-5'-triphosphate (GTP) to ATP and GTP, respectively. This investigation was conducted to determine the significance and applicability of these productivity indices in studying the relationship of production and distribution of micro-plankton (principally algae) to frontal features in the coastal upwelling zone. The highest concentration of biomass associated with the highest rate of absolute productivity was preferentially located in the strong thermo-nutrient gradient in the warmer stratified water at the equatorward edge of the feature.

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ACKNOWLEDGMENTS

Research for this thesis was conducted as part of the ongoing chemical mesoscale research project headed by Dr. Eugene Traganza under the cognizant authority of the Office of Naval Research, NSTL, Bay St. Louis, Mississippi. I wish to take this opportunity to thank my advisor, Dr. Eugene Traganza, Department of Oceanography, for his advice, assistance, and support during every phase of research for and preparation of this thesis.

Special thanks to Mr. Dana M. Austin, Department of Oceanography, whose laboratory expertise, unflagging assistance, and patience proved invaluable to successful completion of this thesis. I would also like to acknowledge Ms. Andrea McDonald, Physics and Chemistry Department; Ms. Bonita Hunter, Oceanography Department; Captain W.W. Reynolds and the crew of the R/V ACANIA; and Mr. Larry Breaker of the National Environmental Satellite Service, at Redwood City, California, for their assistance and support. Lastly, I would like to thank Dist. Prof. Eugene C. Haderlie, Department of Oceanography, for his constructive evaluation of the final manuscript.

I. INTRODUCTION

A. SPATIAL DISTRIBUTION OF BIOMASS AND PRODUCTIVITY

This thesis examines the distribution and production of micro-organisms within a coastal upwelling front located off Pt. Sur, California. Underway measurements of adenosine-5'-triphosphate (ATP) and pigment fluorescence (principally chlorophyll a) were used to estimate the amount of living biomass present at 2.5 m. Specific (mg C mg Chla^{-1} h^{-1}) and absolute (mg C m^{-3} h^{-1}) productivity were measured by a new method using the nucleotide ratio of guanosine-5'-triphosphate (GTP) to ATP and GTP, respectively. Currently there is no measure of productivity which can easily be applied to large numbers of samples in the field. It was the aim of this thesis to evaluate this new technique to determine if the GTP/ATP ratio would prove to be a viable alternative to ^{14}C uptake measurements in the field. Therefore, investigations were conducted to determine the significance and applicability of the productivity indice, GTP/ATP, to a study of the relationship of production and distribution of microplankton (principally algae) to frontal features in the coastal upwelling zone.

The patchy distribution of plankton arises from the irregular structure of many ocean variables. Thus distribution is directly affected by factors such as the intensity of mixing and stratification of waters, advection

and turbulent diffusion (which alter the physical and chemical boundary conditions by varying light, temperature, and salinity gradients), rate of phytoplankton growth, and zooplankton predation patterns [Ref. 1]. Growth or productivity is primarily affected by the rate of entry of nutrients into the photosynthetic layer, available insolation, and variations in the physical environment produced by fluctuations in the winds and currents [Ref. 2].

Various studies have been initiated to try to understand the patchy distribution of biomass and the dynamics which are involved in producing this heterogeneous regime. It is logical to assume that the dispersal of phytoplankton would be controlled to some extent by the physical dynamics of their fluid environment. Some studies of oceanic water which have examined the spatial heterogeneity of biomass have found little evidence of any identifiable structural relationship [Ref. 3, 4, 5]. The lack of information about the vertical structure generally limits inferences which can be made about the observed horizontal variability.

It may very well be the inhomogeneities in the environment which produce the patchy character of the phytoplankton and in turn the patchy zooplankton distribution, which ultimately ensure the stability of the system. One laboratory study which supports this view investigated limiting nutrient patchiness in an ammonia limited continuous culture and found that organisms were best able to

utilize their environment, determined by maximal uptake rate, in a patchy nutrient regime [Ref. 6].

Areas of oceanic fronts, however, appear to exhibit some consistent structural relationships between the location of phytoplankton biomass and physical and chemical variables. Although different mechanisms are involved in the generation and maintenance of frontal boundaries (which are produced by upwelling, eddies, and the lateral juxtaposition of adjacent water masses), the generation of strong thermal and chemical gradients indicates that these are likely to be regions of high productivity where a large standing crop will be concentrated.

The following studies, both observational and theoretical, provide supporting evidence for the preferential occurrence of biomass in or adjacent to frontal boundaries.

The region southwest of Pt. Sur, California, has been shown to be an active area of frequent upwelling advancing the theories of earlier investigators who proposed that the phenomenon of upwelling is intensified equatorward of capes and points along west coasts in both hemispheres [Ref. 7]. Previous research investigating features occurring in this region suggests that biomass is preferentially located adjacent to frontal boundaries defined by strong gradients of nutrients and temperature [Ref. 8, 9]. It is not presently known whether this apparent relationship is simply the result of dynamic processes physically

accumulating biomass through the horizontal and vertical movement of water parcels at this location, or if the conditions produced by the upwelling feature itself provide optimal conditions for growth through formation of a "natural chemostat" [Ref. 10, 11, 12].

Plankton have been found to be concentrated at the frontal boundary of a warm-core eddy in the southwest Tasman Sea [Ref. 13]. Seasonal thermal fronts occur in the western Irish and Celtic Seas. The western Irish Sea front is a shallow front which is a zone of transition between mixed and stratified waters. An investigation of the microvariations occurring at the front noted increases in biomass at the front, measured by chlorophyll *a*, peaking on the western edge in the warmer stratified waters. Microbial activity, measured through urea utilization was found to be highest at the front itself [Ref. 14]. The relationship between biomass location, measured by concentrations of chlorophyll *a*, and primary productivity, measured by the carbon-14 uptake method, was studied in the Celtic Sea [Ref. 15]. Increases in both biomass and productivity were found at the thermal discontinuity. A persistant salinity front occurs in Liverpool Bay. It has been shown that a marked increase in biomass, measured by chlorophyll *a*, and growth, by increases in primary productivity and Assimilation Index, occurs at the front [Ref. 16]. The frontal boundaries which occur in the

southwest approach to the English Channel have not only been found to be sites of high phytoplankton production but under the right conditions red tides may develop. The highest values of chlorophyll *a* were found to extend into the stratified side of the frontal boundary [Ref. 17].

Further evidence supporting these *in situ* observations has been advanced through satellite imagery. SKYLAB observations of the spectral properties of upwelled waters off the northwest coast of Africa found a strong correlation between ocean color ratio gradients, which are indicative of productivity, and sea surface temperature gradients. Ground truth data supported these findings [Ref. 18]. Similar structure has been observed in features occurring off Pt. Sur, California. Satellite information from the NIMBUS7 CZCS (Coastal Zone Color Scanner) which has been corrected to show the visible spectral properties associated with the pigment chlorophyll *a* have confirmed the presence of biomass on the equatorward edge of a cyclonic feature in June 1980 [Ref. 19]. These satellite images confirmed previous interpretation of surface contours which were constructed using *in situ* data [Ref. 20] which had suggested the presence of such structure.

One simulation study examined phytoplankton patchiness using a spatial model in which an initial phytoplankton patch was subjected to the stresses existing in the natural oceanic environment (turbulent diffusion, nutrient limitation, diurnal variations, and nocturnal or continuous

grazing). This model was numerically integrated for several oceanic states. One case of interest examined an oceanic region where abundant nutrients were homogeneously distributed. The immediate consequence was the appearance of a phytoplankton bloom which proliferated as it diffused into the nutrient rich water. An interesting result of this case was the appearance of sharp gradients in the nutrient field near the edge of the phytoplankton patch [Ref. 21].

The three-dimensional spatial structure of the biological community is extremely complex. Through increased appreciation and understanding of the three-dimensional interactions and identification of the controlling mechanisms which operate in areas of oceanic fronts such as in the relatively contained region where upwelling is occurring, it may be possible to extend these insights to diverse oceanic areas.

B. GUANOSINE TRIPHOSPHATE

1. The Role of GTP in Protein Synthesis

Because of its crucial role in protein biosynthesis, the intracellular concentration of GTP fluctuates in direct proportion to the increases or decreases in ribosome synthesis and thus growth [Ref. 22]. Therefore, the ratio of GTP to ATP has been proposed as an index of potential growth representing the instantaneous productivity per unit biomass [Ref. 23, 24].

Guanosine triphosphate (GTP) is an essential factor required for protein biosynthesis. Its presence is needed to initiate synthesis, for aminoacyl transfer ribonucleic acid (tRNA) binding to ribosomes, in translocation and elongation processes, and in the termination of the polypeptide chain. During each of these processes GTP is hydrolyzed. No evidence exists for its use in the formation of any covalent bond, so it does not act like an ATP energy donor. In both bacteria and eukaryotes, the binding and release of initiation factors from ribosomes occurs only when all of the components of the initiation complex are present, one of which is GTP. Since initiation is just the first event which begins protein synthesis, GTP is only significantly hydrolyzed during aminoacyl-tRNA binding and translocation processes. After the first aminoacyl-tRNA bond has formed, the acceptor site is blocked by the tRNA. Until this tRNA is translocated and a new codon on the ribosome is exposed, the site cannot accept an additional aminoacyl-tRNA and peptide synthesis is halted. GTP is one factor which is involved in transferring the peptidyl tRNA to a donor site, freeing the acceptor site to receive another aminoacyl-tRNA complex [Ref. 25]. GTP thus plays an important role in the noncovalent binding of the translocational factors to the ribosomal surface. Splitting of the high energy phosphate bond is necessary for the movement. Based on

experimental evidence, one GTP molecule is hydrolyzed for every translocation act. During the elongation process of protein biosynthesis in prokaryotic systems, a ternary complex is formed, consisting of an elongation factor, GTP, and aminoacyl-tRNA. This complex binds to the ribosome, GTP hydrolysis occurs, and a new peptide bond is formed [Ref. 26]. During the elongation of a polypeptide chain, two molecules of GTP must be hydrolyzed for every one molecule of amino acid which is incorporated [Ref. 27]. For polypeptide chain termination the presence of a GTP-bound release factor is necessary [Ref. 28]. Protein inhibitors suppress nucleotide synthesis, reducing the availability of newly synthesized GTP and CTP (cytosine triphosphate), and thus the subsequent incorporation of GTP into RNA and of d-GTP (deoxy-guanosine triphosphate) into DNA [Ref. 29].

2. GTP as a Measure of Productivity

The combined supply of nutrients available for the synthesis of new organic matter and the availability of energy for photosynthesis in the form of insolation determines the upper limit of productivity for a particular marine ecosystem. Growth, defined as an increase in phytoplankton substance, measured by carbon-14 uptake (g ^{14}C m^{-1} d^{-1}) has been well documented. The assumption is that carbon-14 uptake measures the net increase in new particulate cell carbon [Ref. 30, 31, 32]. This method,

although well established, is time-consuming and difficult to apply in the field.

Studies which have measured both growth rate and nucleotide concentrations of micro-organisms tend to support the hypothesis that the ratio of GTP to ATP can be equated to a measure of productivity or growth rate such as doublings per hour. Most confirm that the relative amounts of ATP present per unit biomass remain constant, since this level is maintained independent of growth, while the levels of GTP per unit biomass increase. A study of the growth rate of the cyanobacterium *Anacystis nidulans* grown at different light intensities exhibited an exponential decrease in the GTP concentration per unit biomass with decreasing growth rate while the ATP levels per unit biomass remained relatively constant [Ref. 33]. A similar decline in GTP levels per unit biomass was reported by Sokawa [Ref. 34] in his studies of *Escherichia coli*.Inversely, Franzen and Binkley have shown GTP levels per unit biomass to increase with growth while ATP levels per unit biomass remain constant in this species [Ref. 35]. In another study which measured GTP in micromoles per gram of dry weight as a function of growth rate in the bacteria *Salmonella typhimurium*, GTP per unit biomass increased with increasing growth rate (although a simple relationship could not be deduced) while ATP levels per unit biomass remained constant for all media "except in the broth where it doubled" [Ref. 36].

A field study of the vertical distribution of biomass and productivity in the waters of the Black Sea found simultaneous increases in biomass (ATP), metabolic activity (measured by the energy charge), and growth (measured by the ratio of particulate nucleic acids to ATP) in the anoxic region of this water body [Ref. 37]. Results reported in a later study showed a similar increase in the productivity ratio, GTP/ATP, at similar depths [Ref. 38].

II. METHODS

A. CRUISE STRATEGY

One purpose of this thesis was to study the distribution and productivity of microplankton within areas of strong thermal gradients. To accomplish this goal, data were acquired from the Naval Postgraduate School's research vessel R/V ACANIA during 27-29 October 1980 in an area located southwest of Pt. Sur, California, which is known to be a region of recurrent upwelling events. Measurements of adenosine-5'-triphosphate (ATP) and chlorophyll a were used to estimate the amount of living biomass present. Productivity was determined using a new technique, viz., the enzymatic determination of the nucleotide ratio of guanosine-5'-triphosphate (GTP) to ATP.

Another purpose was to gain some insight into the biological significance of this ratio, and to investigate its applicability as a measure of microplanktonic productivity. To study these questions two experiments were performed. The first, a field experiment, compared carbon-14 (^{14}C) uptake and assimilation numbers (mg ^{14}C mg $chla^{-1}$ hr^{-1}) to GTP and the GTP/ATP productivity ratio, respectively. The second experiment related rates of protein synthesis inferred from the relative RNA (ribonucleic acid) to DNA (deoxy-ribonucleic acid) ratio for different population

groups of Tigriopus californicus to the GTP/ATP ratio of similar groupings in order to determine if this productivity index is relevant to zooplankton.

Prior to and during the October 1980 cruise, satellite infrared imagery of the area of interest was relayed to the scientific party by Mr. Larry Breaker, the staff oceanographer for the National Environmental Satellite Service (NESS) office located in Redwood City, California. The images provided the location, orientation, and dimensions of the feature of interest as well as the apparent strength of the associated thermal gradients which defined the upwelling area. This information proved invaluable for initial location and for designing a cruise track for optimal underway sampling strategy. Most of the sampling effort was concentrated near the equatorward boundary of the feature extending into the stratified waters of the surrounding region. This strategy was principally designed to select prime transects through areas of strong thermal gradients to investigate the levels of biomass and productivity within and adjacent to these areas. Subsequent to the completion of the cruise, enhanced satellite imagery coincident with the cruise dates was fowarded for project documentation. The proposed cruise track was zoom-transferred onto an image (Plate 1) of the California coast, taken 29 October 1980. This view proved useful in interpreting ground truth data. Outer track positions are indicated for orientation (refer to Fig. 1, 2).

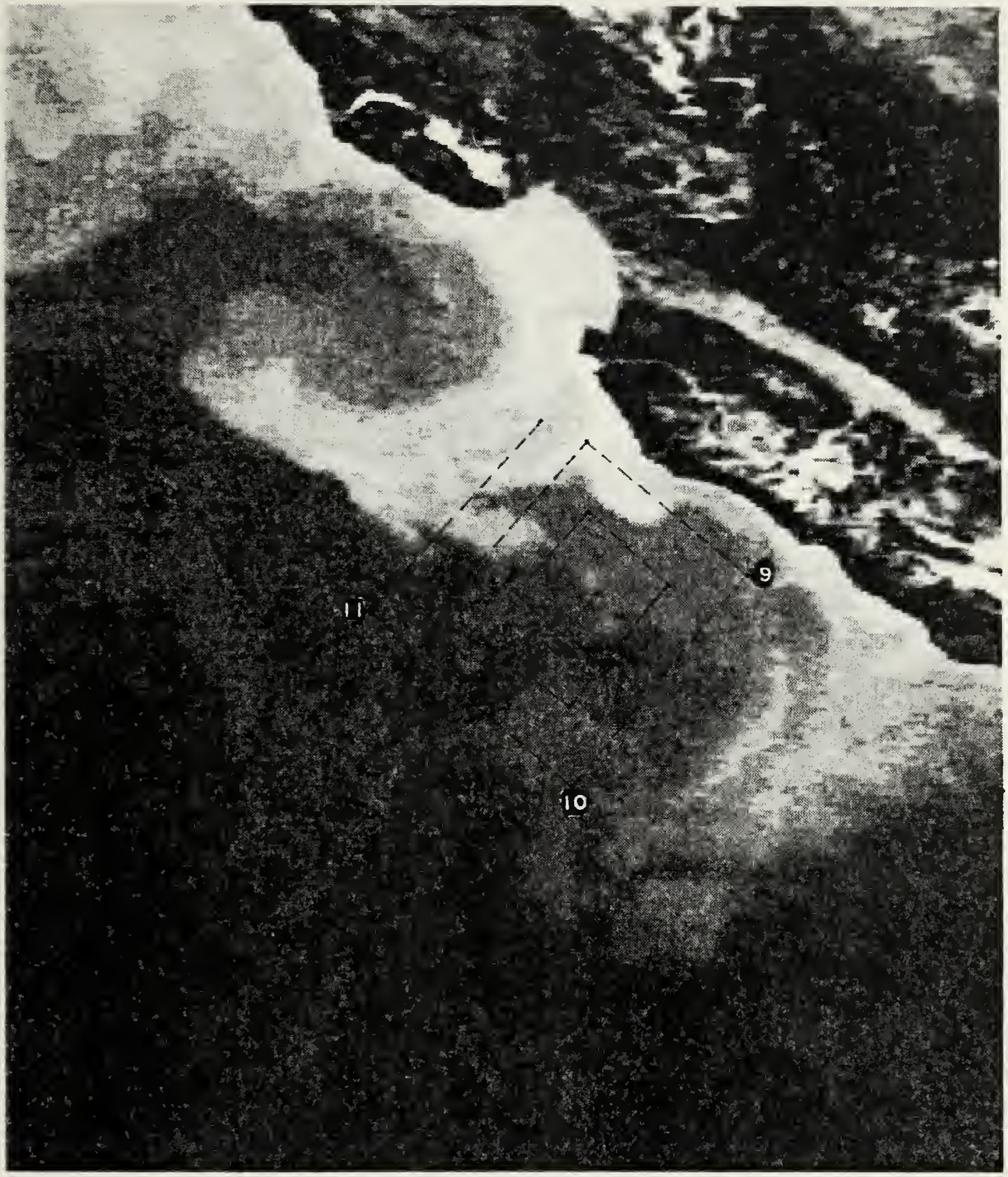

Plate 1. TIROS Satellite IR image of the California coast, 29 October 1980.

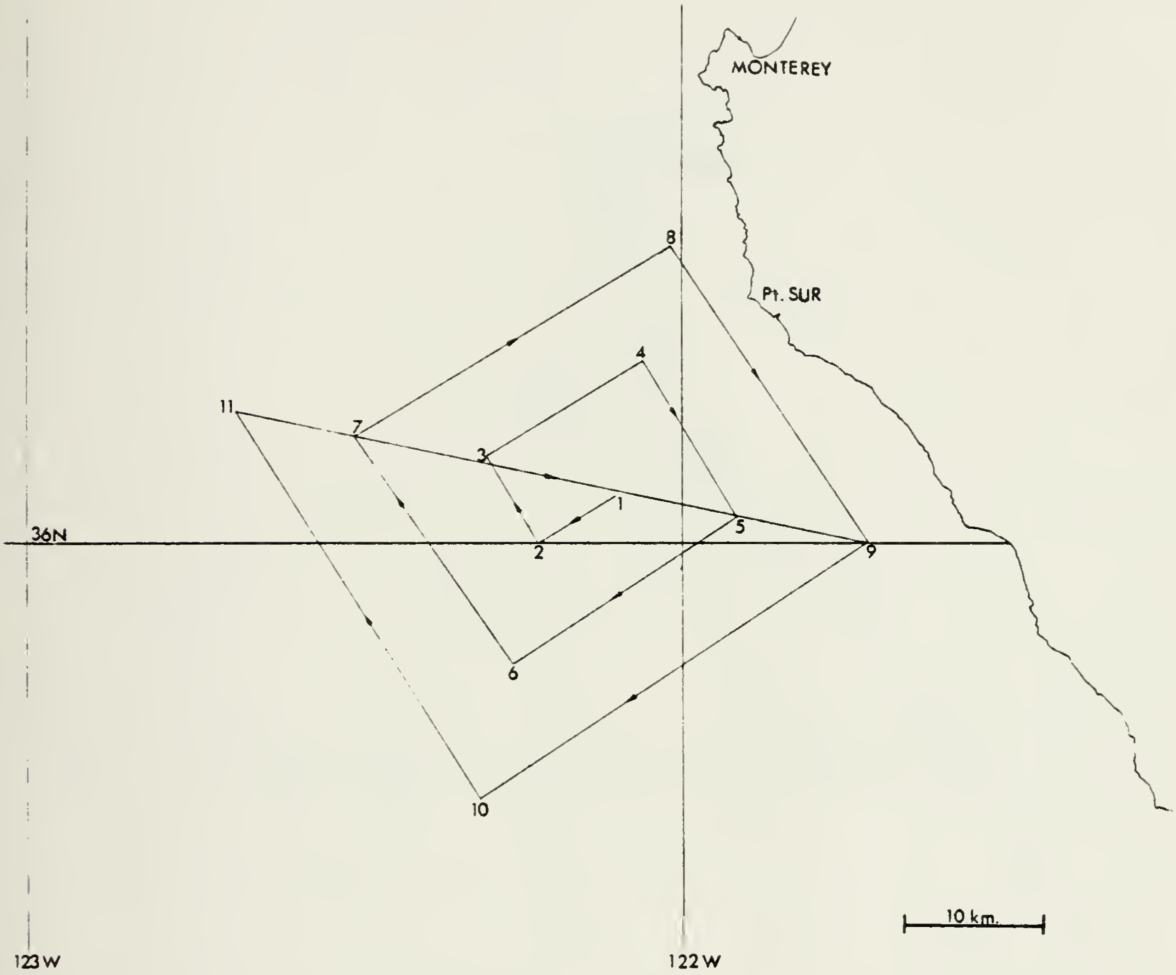

Figure 1. Cruise Track for 27-28 October 1980.
Scale 1:216,116

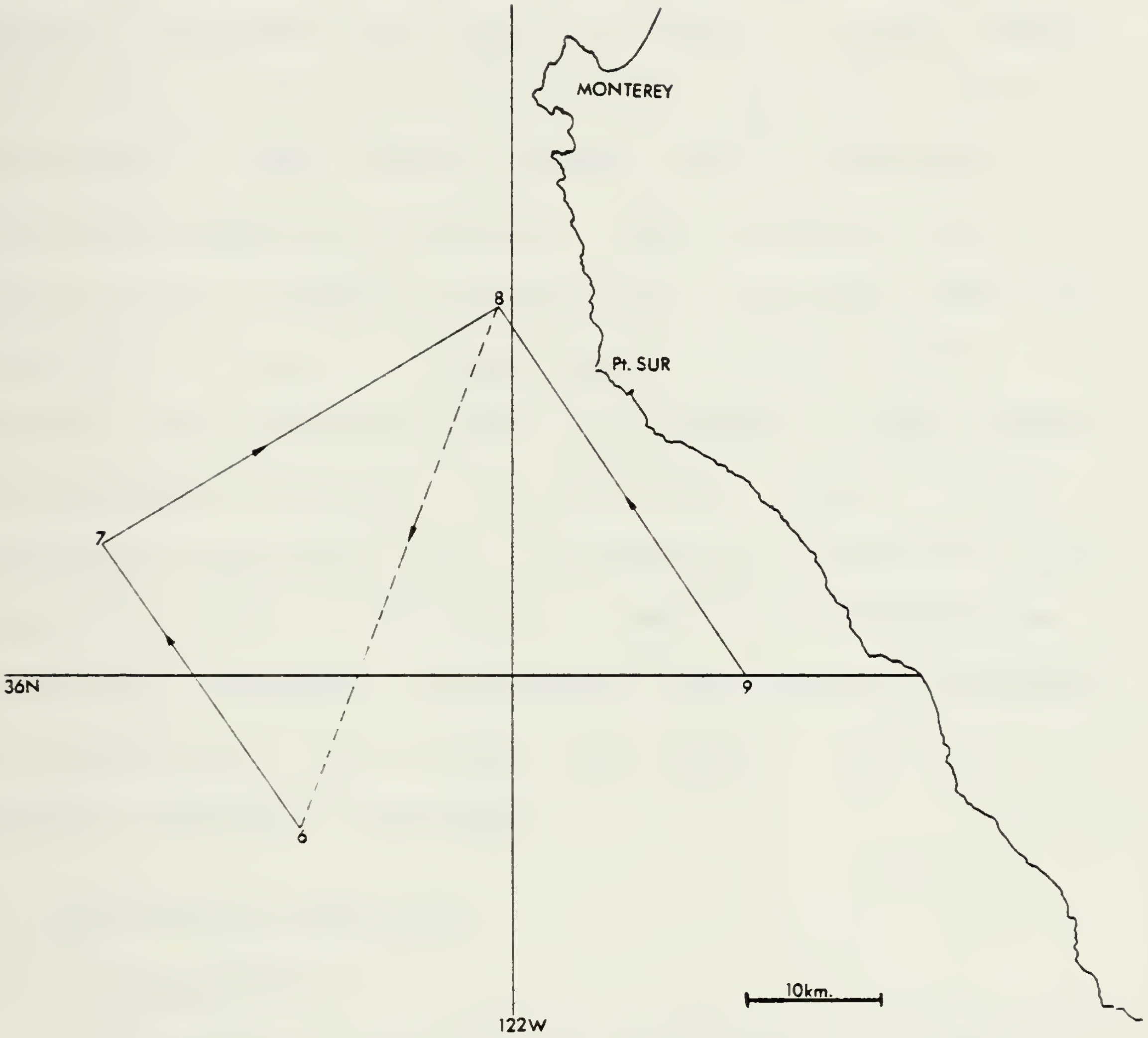

Figure 2. Cruise Track for 29 October 1980.
Scale 1:216,116

Once in the area, the cruise track on 27-28 October was an expanding square (Fig. 1). Table I gives navigational positions for this portion of the cruise track.

A continuous record of temperature and fluorescence pinpointed the areas of sharp gradients and high biological activity validating the satellite imagery. The R/V ACANIA used Loran C to fix its position every half hour, while maintaining a speed varying between six to nine knots during the transit of each leg. Once the feature and areas of prime interest were defined, the cruise track on October 29th (Fig. 2) followed prime transects which allowed a more detailed view of the feature's major chemical and biological structure to be obtained. Table II gives navigational positions for this portion of the cruise track. During this phase of operations, the dissolved nutrients-nitrate and phosphate, fluorescence, and sample collections for chlorophyll, ATP, and GTP were taken, and the Carbon-14 experiment was begun.

B. MEASUREMENT TECHNIQUES

1. Temperature

Temperature was measured continuously *in situ* by a thermistor immediately adjacent to the pump intake located in a sea chest at a depth of 2.5 meters. A strip chart recording was later calibrated through the use of bucket thermometer readings which were taken every half hour.

TABLE I

Track Positions for 27-28 October 1980

Date	Position Identification	GMT	Latitude	Longitude
10/27/80	1	0520	36°03.8'N	122°06.0'W
	2	0646	36°00.0'N	122°13.1'W
10/28/80	3	0743	36°06.5'N	122°17.9'W
	4	0919	36°13.7'N	122°03.6'W
	5	1050	36°02.1'N	121°54.9'W
	6	1315	35°51.0'N	122°15.2'W
	7	1546	36°08.0'N	122°29.5'W
	8	1847	36°22.1'N	122°01.0'W
	9	2157	36°00.1'N	121°42.9'W
	10	0156	35°40.9'N	122°18.3'W
	11	0519	36°05.2'N	122°36.4'W

TABLE II

Track Positions for 29 October 1980

Date	Position Identification	GMT	Latitude	Longitude
10/29/90	9	1646	35°59.9'N	121°42.9'W
	8	1946	36°22.1'N	122°01.0'W
	6	2335	35°50.7'N	122°15.4'W
	7	0200	36°07.9'N	122°29.5'W
	8	0500	36°21.0'N	122°02.8'W

2. Plant Pigments (Principally Chlorophyll a)

Seawater was pumped from the keel intake to the dry lab where a debubbler removed air bubbles from the water in the line before it was shunted to the fluorescence measuring device. A Turner III Fluorometer provided a continuous record of fluorescence,which was later calibrated following the procedures outlined by Lorenzen [Ref. 39], using concentrations of discrete chlorophyll a samples. The basic assumption of *in vivo* fluorometry is that there is a constant ratio between the fluorescence of an *in vivo* sample and the extractable chlorophyll a pigment. This value is the calibration ratio of the instrument, which is subsequently used to approximate the chlorophyll a concentration. This assumption does not always provide accurate information. Fluorescence can vary by a factor of two to five for a fixed chlorophyll a concentration when phytoplankton are exposed to varying conditions [Ref. 40]. Seawater samples of 275 ml each were taken in triplicate hourly from the debubbler outflow. Each sample was vacuum filtered through a Whatman G/FC glass fiber filter with a pore size of approximately 0.45 μm. These filters are able to separate phytoplankton and other larger organisms. The filters were folded, placed in polyethelene bags labeled with the time and ship's position, and stored frozen at -30°C until analyzed according to the procedures outlined by Strickland and Parsons [Ref. 41].

3. Nutrients

A Technicon Autoanalyzer AA-II (Technicon Corporation, Tarrytown, New York) was used to colorometrically determine the reactive inorganic phosphorus and nitrogen in the surface water (2.5m) at a sampling rate of once every two minutes in accordance with the procedures outlined in [Ref. 42, Ref. 43, Ref. 44]. Cadmium columns were packed and conditioned for nitrate analysis in accordance with the procedures detailed in Ref. 45. The autoanalyzer reduces the nitrate to nitrite before measurements are made. Therefore traces of nitrite in the upper portion of the water column could erroneously elevate the levels of nitrate recorded. According to Paulson [Ref. 46] this error would be unlikely, since his studies of the nutrient variations in this area have indicated that there is almost no interference from surface nitrite.

4. ATP and GTP

Vacuum filtration is the most practical and effective method of cell concentration but, it also has a detrimental effect on the concentration of ATP [Ref. 47]. Therefore, a minimal sample extraction volume of 50 ml was used for concentration and subsequent extraction of the nucleotides in order to reduce the effects of the filtration procedure. To determine ATP, ΔATP, and GTP at a later date these 50 ml sample volumes which had been prefiltered through a 200μm nylon screen were vacuum filtered

through a microfine glass fiber filter (Reeve Angel 984-H with a pore size of approximately 0.45 µm). This filter is capable of separating algae, microzooplankton, and marine bacterial cells. Immediately after the final amount of liquid had passed through the filter, the vacuum was released and the filter quickly immersed in 10 ml of boiling Trizma (Tris (hydroxymethyl) aminomethane and hydrochloride) buffer (pH 7.7) in order to extract the nucleotides present in the water sample. The test tubes containing the extracts were labeled and stored frozen at -30°C for later analysis.

C. LABORATORY ANALYSES

1. Theory of ATP Analysis

The ATP concentration in microplankton (algae, microzooplankton, and bacteria) is a reasonably good measure of the total living organic cellular carbon present /‾Ref. 48_7.

The amount of ATP present within a given sample is determined by the amount of light emitted during a bioluminescent reaction catalyzed by luciferase, Fig. 3.

In the first reaction, luciferin reacts with ATP in the presence of magnesium producing the bound luciferyl adenylate which then reacts with oxygen to form oxyluciferin, carbon dioxide, adenosine monophosphate and light /‾Ref. 50_7. According to the kinetics of this reaction the quantum yield of visible light as measured by Seliger and McElroy

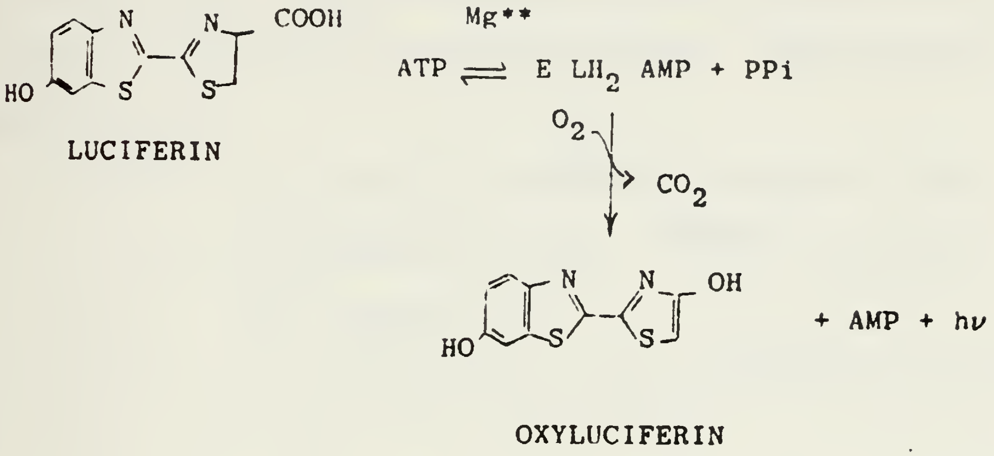

Figure 3: ATP luminescent reaction (from DeLuca [Ref. 49])

where E-LH2-AMP is the bound luciferyl adenylate; PPi, inorganic pyrophosphate; O_2, oxygen; CO_2, carbon dioxide; AMP, adenosine monophosphate; hv, light

[Ref. 51] is of the order of 0.88 emitted for each ATP molecule which is hydrolyzed [Ref. 52]. Concentrations of ATP can be determined by comparing the light emitted (counts per minute) by the standards with that of the unknown samples.

2. Theory of GTP Analysis

GTP was determined by the method outlined by Karl [Ref. 53]. GTP is measured using an NDPK (nucleoside diphosphate kinase-firefly luciferase) coupled bioluminescent reaction. In this method GTP is transphosphorylated to an

equivalent amount of ATP. The concentration of ATP is then determined by the amount of light produced when it is reacted with a crude substrate-enzyme mixture of firefly luciferase-luciferin as described above. The pertinent reactions are:

1. D-glucose + ATP $\overset{\text{HK}}{\rightleftharpoons}$ D-glucose 6-P + ADP + H^+
2. D-glucose 6-P $NADP^+$ $\xrightarrow{\text{G6P-DH}}$ gluconate 6-P + NADPH + H^+
3. α-D-glucose 1-P + UTP $\xrightarrow{\text{UDPG-PP}}$ UDP-glucose + PP_i
4. ADP + GTP $\overset{\text{NDPK}}{\rightleftharpoons}$ GDP + ATP
5. ATP + luciferin $\xrightarrow{\text{L}}$ product + PP_i + light

where HK is hexokinase; G6P-DH, glucose-6 phosphate dehydrogenase; UDPG-PP, UDP-glucose pyrophosphorylase; UTP, uridine triphosphate; PP_i, inorganic pyrophosphate; NDPK, nucleoside-5'-diphosphate kinase; and L, firefly luciferase.

Reactions (1) and (2) eliminate all of the ATP present within the sample extracts, preventing any interference from this nucleotide in the quantitative assay of GTP. Reaction (1) removes a phosphate from an ATP molecule and transfers it to D-glucose producing D-glucose-6-phosphate and ADP. Reaction (2) oxidizes D-glucose-6-phosphate to gluconate-6-phosphate and simultaneously reduces $NADP^+$ to NADPH. Reaction (2) drives reaction (1) to completion

ensuring that all the ATP in a given sample extract will be converted to ADP. In reaction (3), a phosphate is removed from UTP forming UDP which is combined with a glucose molecule from the D-glucose-1-phosphate to form UDP-glucose, thus effectively preventing interference from UTP. In reaction (4), a phosphate is transferred from GTP to ADP in the presence of excess ADP producing one molecule of ATP for each GTP molecule which is transphosphorylated. The assay for GTP is based on the linear luminescent response of crude firefly lantern extracts to the addition of ATP (produced in reaction (4)). In reaction (5) ATP in the presence of the luciferin/luciferase enzyme preparation gives off light which is then measured by a photometer. This method is sensitive to picomolar (pM) concentrations of GTP [Ref. 54].

3. Procedures for GTP Enzymatic Conversion

For the GTP determination, 0.8 ml of each sample extract was pipetted into a series of disposable glass cuvettes (12x75mm) and placed in a test tube rack in an incubating water bath at 30°C. Each tube was allowed to come to temperature and then 0.2 ml of an enzyme solution containing 75mM potassium phosphate buffer (pH 7.4), 15mM $MgCl_2$, 0.5 mM NADP, 0.5mM d-glucose, 0.5 mM α-D-glucose-1-phosphate, HK/G6P-DH (2 units/ml), and UDPG-PP (5 units/ml) was pipetted into each vial. To obtain the proper proportions, four separate solutions were prepared as follows:

1. A 60 mM solution of $MgCl_2$ was prepared adding 5 ml of distilled H_2O to .13g $MgCl_2$

2. A 300 mM solution of K_2PO_4 was prepared by adding 5 ml of distilled H_2O to .261g K_2PO_4

3. A 2mM solution of D-glucose and α-D-glucose-1-phosphate was prepared by adding .01802g of D-glucose and .03363g of α-D-glucose-1-phosphate to 50 ml H_2O ("nanopure")

4. A 2mM solution of $NADP^+$ was prepared by adding 3.1 ml distilled H_2O to a preweighed vial containing 5 mg NADP

Then 2.5 ml of each of the above four solutions were combined to produce a total solution of 10ml to which .236mg HK/G6P-DH and 12.5mg UDPG-PP was added. This produces a final enzyme solution with the desired colarities and required activity levels. Each vial was swirled to mix the reactants and then allowed to react at 36° C for 15 minutes. The enzymes were then deactivated by placing the culture tubes in a boiling water bath (100°C) for three minutes to ensure that the GTP would not in time be hydrolyzed enzymatically. The rack was then removed from the boiling water bath and the cuvettes were allowed to come to room temperature (25°C) at which time they were sealed with parafilm and stored frozen at -30°C until analyzed.

An experiment was conducted similar to one performed by Karl [Ref. 55] to confirm that these procedures would produce the desired enzymatic reactions. The enzymatic procedures outlined in the preceding paragraph

were followed using 0.8ml of 2×10^{-7} M solutions of GTP and ATP. The 30°C reaction times were allowed to vary. These were zero, 2 min., 4 min., 8 min., 10 min., 20 min., and 30 min. Percent light emission for both ATP and GTP were plotted as a function of reaction time (Fig. 4). The concentration of solutions composed of 0.8 ml of ATP and GTP, respectively, to which 0.2 ml of Trizma had been added were used as the maximum to which all other values were normalized when percent light emission was calculated. The ATP levels dropped to zero after four minutes indicating that all interference from the ATP had been eliminated from the sample as anticipated. The GTP levels remained relatively constant as expected. For the zero reaction value the percent light emission is only about 46% vice 100% because it took a small amount of time before the mixture could come to deactivation temperature in the boiling water bath and halt the reaction. This delay was enough to significantly reduce the levels of ATP present within the sample. Had the enzyme preparation been injected into a sample which had already come to deactivation temperature the reaction would not have been allowed to proceed and the percent light emission would have been more nearly 100%. The experiment confirmed that the enzymatic procedures do in fact eliminate all interference from ATP which may be present in a sample extract.

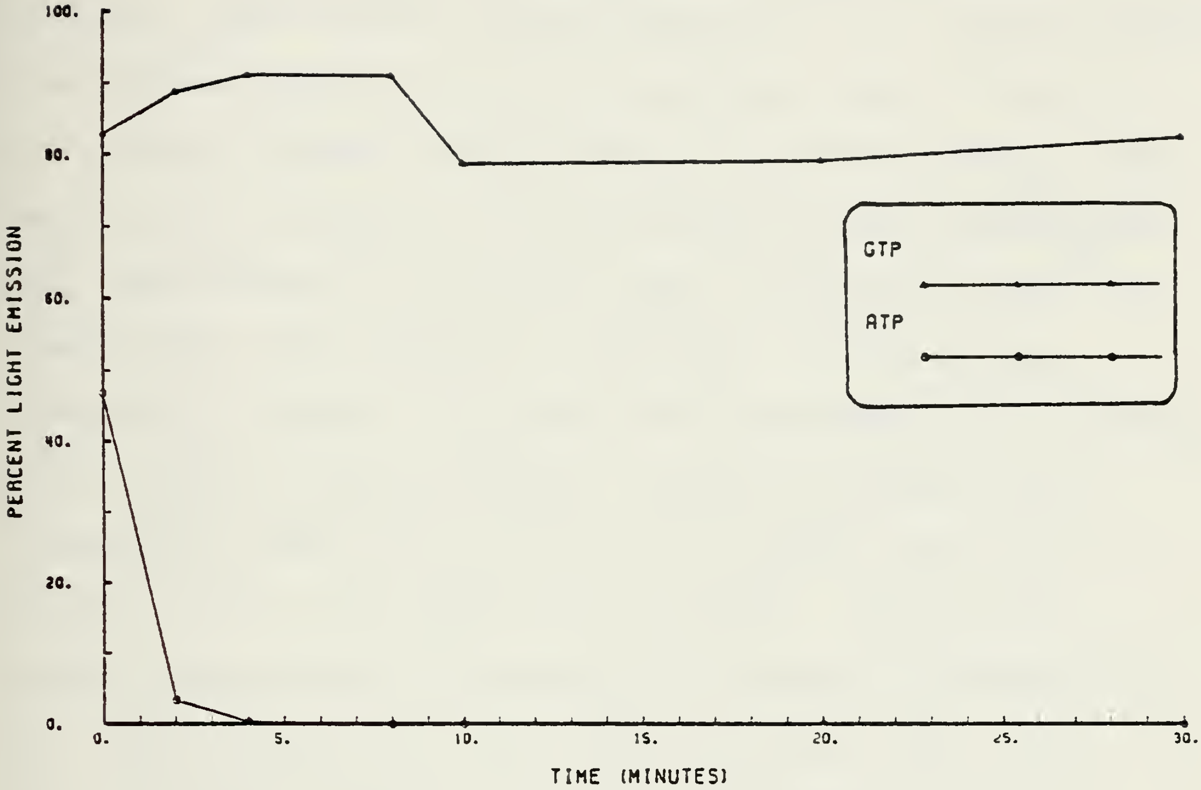

Figure 4. Kinetics of ATP and GTP reactivity for the Hexokinase/glucose-6-phosphate dehydrogenase coupled reaction.

4. Procedure for Photometric Determination of ATP or GTP

a. Enzyme Preparation

Each vial of lyophilized firefly lantern extract, Sigma FLE-50 (Sigma Chemical Co., St. Louis, Missouri), was reconstituted with 5 ml of distilled water, 10 ml of .1M arsenate buffer (pH 7.4), and 10 ml of .04 M $MgSO_4$. This mixture was allowed to sit in the dark at room temperature for approximately 16 hours in order to allow the level of background light emission to subside. To remove the insoluble residue, the enzyme was centrifuged for 15 minutes. It was then filtered through a Whatman #2 paper filter. Immediately before use, 500 μg of luciferin and 25 ml of Trizma (.02 M) were added to the bottle. Spiking the enzyme preparation with exogenous luciferin increases the net light emission per unit ATP in solution [Ref. 56]. This increased reactivity allows subpicogram levels of ATP to be detected, which in practice allows a 50 ml sample of seawater to be used. A larger volume would take too long to filter because stress produced on the organisms would cause them to alter their ATP levels (therefore, their GTP/ATP ratio would be suspect).

When the luciferase enzyme was being prepared for a GTP assay, the enzyme preparation was saturated with ADP using 10.0 μg. The enzyme preparation was mixed and stored in a 250ml plastic bottle to lessen the decay rate which was found to be significant in glass containers

/‾Ref. 57_7 due to shearing of the enzyme molecules which occurs at the glass-liquid interface. The assay was carried out under reduced lighting conditions to minimize the destructive effects of normal laboratory lighting on the enzyme preparation.

b. ATP and GTP Analysis

Both ATP and GTP concentrations were analyzed using the light dependent reaction of ATP in the presence of the luciferin/luciferase enzyme preparation. The amount of light emitted in this reaction is proportional to the concentration of ATP in the unknown sample. The total measuring system was designed and engineered by Biospherical Instruments, Inc., San Diego, California. The primary components include an Industrial Micro Systems 5000 Microcomputer; a SOROC IQ-120 CRT terminal; an Anadex DP9500 Dot Matrix Printer with extended buffer; an ATP integrating photometer, SAI model 3000, with an automatic pipette; software programs on five inch diskettes which control individual runs and perform the required calculations. A strip chart recorder was interfaced with the photometer to monitor the reaction kinetics. From observation of the kinetics it was possible to determine if the enzyme was stable from one sample to the next, if the pipette tip dripped and a drop of the enzyme solution initiated the reaction prematurely, and in the GTP determinations, if there was any residual interference from ATP which would appear as an initial peak.

During each run 0.2 ml of an unknown or standard solution was automatically injected into a polystryene cuvette (10x50 mm) containing 0.5 ml of the enzyme preparation. A collar which was locally engineered to fit inside the photometer held each vial exactly centered ensuring consistant optical conditions from one sample measurement to the next. The reliability of the peak height values depends upon the quick and total mixing of the reactants. This is ensured through the use of an automatic pipette which provides consistant mixing of all samples throughout a run. Actual injection of samples is controlled by the computer. A microswitch in the photometer senses when the shutter is closed, automatically measuring the dark count. When the shutter is opened the computer then measures the enzyme background for five seconds. The sample is then injected. The peak value is recorded in counts s^{-1} based upon the largest 0.33 second count recorded during the first five seconds after injection. Integral light levels are determined from a series of one-second measurements that are scanned by the computer after the desired delay. In accordance with the assay procedures developed for ATP /‾Ref. 58, Ref. 59, Ref. 60_7, a 15 second delay and 60 second assay period were used. The analysis section of the ATP calculation software developed by Biospherical Instruments Inc., San Diego, Ca. uses the measurement of enzyme background level as a method of tracking and

adjusting for the decline in enzyme activity. The relationship between raw counts (uncorrected for endogenous background emission or blank) and standard values is not linear. With increasing time there is a smaller change in counts at lower concentrations than at higher concentrations of ATP. This relationship can be approximated by a second degree polynomial which is used to calculate a completely new standard curve for each sample according to its enzyme background emission [Ref. 61]. This multiple curve fitting is used to compute the integrated and peak values. Counts per minute are then converted into concentration values in units of ng ml^{-1}.

When samples were analyzed,duplicates of each were run. If these values, in counts per minute, did not agree within 10%, a third sample was analyzed. A complete set of nucleotide standards were prepared using the sodium salt of the nucleotide and .02M Trizma. Standards prepared in the following concentrations: .3, 1.,3.,6., 9.,15., and 30. ng ml^{-1} were run at least every two hours. The final values of both ATP and GTP concentrations were the averaged values of the replicates. The ATP values were determined from the peak height measurements in order to reduce the interference of GTP and other nucleotides which may be present within the sample. If integrated light readings are used, the kinetics of the other nucleotides would interfere with the reaction resulting in falsely elevated levels of ATP [Fig. 5].

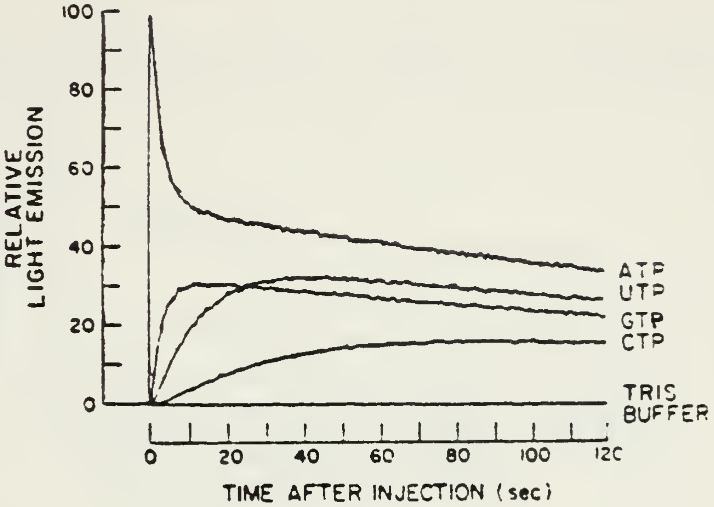

Figure 5: Kinetics of ATP, GTP, UTP, and CTP-dependent light emission using crude luciferase preparations. The concentration of each nucleotide was 4 x 10^{-8} M (from Karl ⁄‾Ref. 62_⁄)

Figure 6 shows the reaction kinetics for varying concentrations of GTP through standard light emission curves. Integral values of light emitted were used to determine the concentrations of GTP present within the samples. Figure 7 shows that either the initial rise, peak, or integrated values can be used to calculate GTP concentrations. Although graphical analyses of integrated light values have been used in the past to calculate ATP concentrations, greater precision is achieved through the use of sophisticated computer software as described above ⁄‾Ref. 65_⁄.

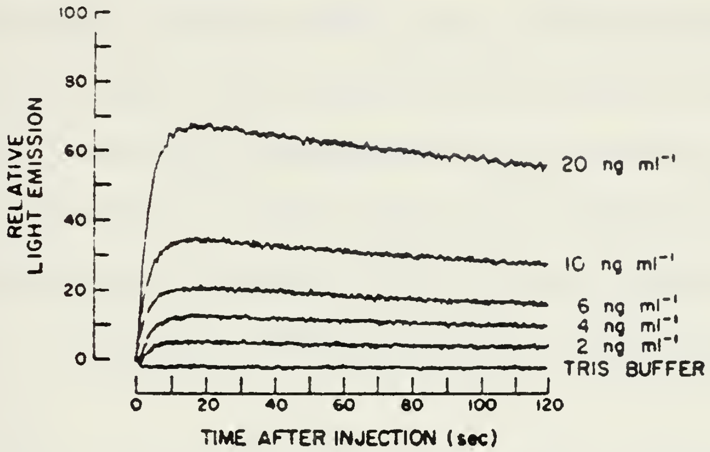

Figure 6: GTP-Dependent Light Emission Standard Curves (from Karl /‾Ref. 63_7)

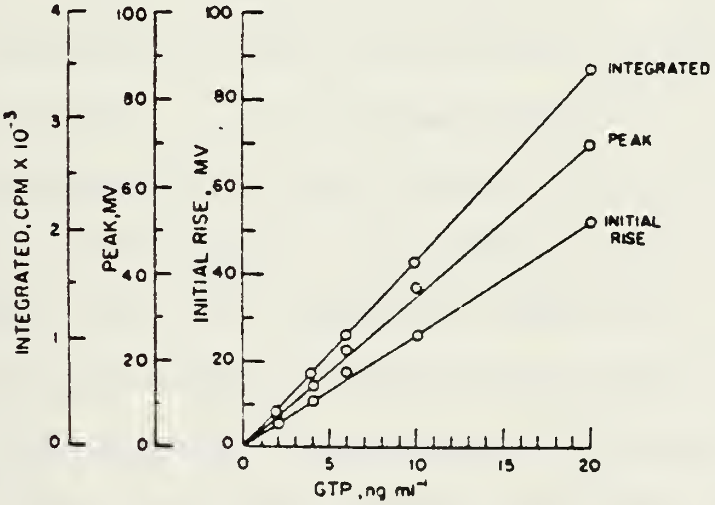

Figure 7: GTP reaction kinetics for samples ranging from 0 to 20 ng/ml of GTP (from Karl /‾Ref. 64_7)

D. CARBON-14 UPTAKE EXPERIMENT

Five water samples were collected at different locations along the October cruise track using a two liter PVC Van Dorn bottle at 1136, 1150, 1339, 1610, and 1933 hours local time. These locations were chosen from observation of the fluorescence record so that areas with differing amounts of biomass could be studied. From these samples, subsamples were taken to determine ^{14}C uptake, ATP, GTP, and chlorophyll a.

Measurement of carbon-14 uptake is the most direct approach used to measure primary productivity. The uptake of $^{14}CO_2$ is considered to be a reasonable indicator of primary production or growth. In this experiment a known amount of radioactive carbon, ^{14}C, was added to three 125ml water subsamples. The ^{14}C was added to the phytoplankton culture in the form of sodium carbonate, $Na^{14}CO_3$), which contained approximately five microcuries of radioactivity per ml per subsample. Two of these subsamples were incubated at surface temperature for approximately four hours on board the R/V ACANIA using a fluorescent light incubator which provided about .06 langley per minute of illumination. The third bottle was kept in the dark and used as a control. To eliminate the contribution of the non-photosynthetic fixation of carbon from the experiment, the dark bottle counts were subtracted from those of the light bottles. After incubation was completed 100ml of each

subsample was filtered and stored in accordance with the procedures outlined by Rowney [Ref. 66] to await shore-based calibration. (Dana M. Austin performed these analyses using a liquid scintillation counter as outlined by Jitts and Scott [Ref. 67]).

Primary production was determined using the following formula from Strickland and Parsons [Ref. 68]:

$$1. \qquad \text{mg C m}^{-3}\ \text{hr}^{-1} = (\text{Rs}-\text{Rb})\ (1.05\text{W})/(\text{RN})$$

where Rs is the radionucleotide activity in the light bottle (CPM); Rb, the dark bottle count (CPM); R, the absolute activity in one ampule (CPM); W, weight of the carbonate carbon in water which is assumed constant at 24,000 mg C^{-3}; N, the number of hours of incubation; 1.05, the isotope discrimination factor. Assimilation numbers (mg ^{14}C uptake mg Chla^{-1} hr^{-1}) were determined using the ^{14}C uptake information and the results of the discrete chlorophyll a determinations.

Measurements of productivity based on ^{14}C uptake and assimilation number were then correlated with GTP and the GTP/ATP productivity ratio, respectively.

E. TIGRIOPUS CALIFORNICUS PRODUCTIVITY EXPERIMENT

Tigriopus californius is a marine copepod found in the splash zone above the mean high water mark along Monterey Bay. Tigriopus californicus hatches from eggs and grows through six naupliar and six copepodid stages,

each of which can be microscopically characterized by distinctive developmental features /‾Ref. 69_7. Research by Baugh /‾Ref. 70_7 related the growth stages of this copepod to the RNA/DNA ratios at various phases in its life cycle.

Since RNA is a necessary ingredient required for protein synthesis, rapidly growing cells contain relatively large amounts of this nucleic acid. In contrast, cells which are growing at a slower rate contain little RNA. A direct correlation between RNA synthesis and protein synthesis has been demonstrated in populations of exponentially growing cells /‾Ref. 71_7.

Sutcliffe /‾Ref. 72_7 showed that this relationship existed in 24 diverse species. Pease /‾Ref. 73_7 was only able to verify these results in the exponential phase of growth. Work by Leick /‾Ref. 74_7 studying bacteria, yeast, and protozoa showed that for a given micro-organism the ratios of RNA to protein and RNA to DNA are linear functions of the growth rate.

Tigriopus californicus were chosen as an experimental organism since data was available on the RNA to DNA ratios for various population subgroups of this species. An experiment was performed to determine if similar trends would be observed in the data when the GTP/ATP ratios were compared to the RNA/DNA ratios for different population subgroups.

Tigriopus californicus were collected with a number 10 plankton bucket from splash pools above the mean high water mark near the Great Tide Pool south of Monterey Bay. Once collected these copepods were kept in plastic containers at 23°C. Individuals were then separated into three experimental groups, similar to those described by Baugh /¯Ref. 75_7. An acryllic separation column with nylon screens was used to separate a mixed population of individuals between 400-500 μm in size. A Pasteur pipette was used to separate an all-gravid female population, the all-but-gravid population were those individuals which were left. Once separated into groups the populations were allowed to rest for two days to recover from the stress of separation in order that their ATP levels would return to normal /¯Ref. 76_7. Immediately prior to extraction the copepods were concentrated by using a 100 μ m nylon screen in the separation column. The organisms were then extracted by immersion in 40ml of boiling Trizma and by simultaneous homogenization with a pestle homogenizer for five minutes. The test tubes were removed and allowed to cool before the extraction fluid was filtered and the filtrate stored frozen at -30°C to await nucleotide analysis. GTP and ATP analyses were performed in accordance with the procedures outlined above. The trend of the productivity ratio, GTP/ATP, was then compared to the trend of the RNA/DNA ratio for similar population groups.

F. DATA REDUCTION

To prepare the data for statistical analysis, the strip chart recordings of fluorescence, temperature, nitrate, and phosphate were hand digitized at a constant interval of two minutes. This sampling interval represents approximately 0.6 km along the cruise track when at full speed.

To generate organic carbon equivalents for comparison of biomass concentrations (determined through ATP and chlorophyll a analyses), the conversion factors originally proposed by Holm-Hansen /‾Ref. 77_7 were used. Determination of these factors was based on exhaustive laboratory observations. These values are nevertheless just averages which can vary depending on species composition and changing environmental conditions /‾Ref. 78_7. Chlorophyll a concentrations were converted to carbon units by using the average conversion factor of 100. ATP values were converted to organic carbon using the average carbon to ATP conversion factor of 250 which is believed to be representative of community microbial biomass (i.e., representing the combined contributions from bacteria, algae, and microzooplankton). In Ref. 79 Holm-Hansen reviews various studies which relate ATP to total cellular organic carbon in a wide variety of fresh and marine organisms giving credence to this average conversion factor. Another study which verifies this conversion factor used direct microscopy to estimate the microbial biomass comparing these values

to those obtained from ATP determinations [Ref. 80]. These investigators found an average conversion factor of 245 for community microbial populations not only in euphotic areas of upwelling but also in the euphotic zone in areas of equatorial divergence, and in aphotic layers. Studies of ATP levels in nutrient-deficient phytoplanktonic organisms have shown some effect on ATP levels, but not enough to significantly affect biomass determinations based on this assay procedure [Ref. 81].

Δ ATP values were computed by subtracting the peak ATP values from the integrated ATP values [Ref. 82]. The Δ ATP and the GTP values were normalized to the biomass by dividing these values by the amount of ATP present within the sample.

Population correlation coefficients were derived using the equation:

$$r = \frac{n \Sigma x_i y_i - (\Sigma x_i)(\Sigma y_i)}{\left(\left[n \Sigma x_i^2 - (\Sigma x_i)^2 \right] \left[n \Sigma y_i^2 - (\Sigma y_i)^2 \right] \right)^{\frac{1}{2}}}$$

Nitrate, phosphate, temperature, biological and productivity indicators were first correlated for all the data points. Then the values were separated into two groups based upon their nitrate concentration. Correlations were then run on these two distinct groups whose separation of values (Fig. 21) suggest the presence of two distinct water masses

during the October 1980 cruise. The implications of the results of these correlations in relation to the biological variables will be discussed in the following chapter.

The standards which were used in determining the GTP concentrations for the cruise data were not treated in a manner similar to the samples. To correct for this systematic oversight an experiment was conducted in which one set of standards was prepared and subsampled into two groups. One group was enzymatically treated, the other was not. The relative activity of GTP in the treated standards was an average of 25.6 percent of the untreated standards. The cruise data were adjusted upwards in accordance with this finding.

III. RESULTS

A. OCTOBER 1980 CRUISE FINDINGS

On the October 1980 cruise, temperature, nutrient, biomass, and productivity data were collected and analyzed. A listing of these data appears in Appendix A. Results presented in this chapter are associated with a minimum of description. Interpretive discussion is reserved for the following chapter. Ranges for the biomass and productivity indicators are given in Table III. Surface maps and linear track plots from this cruise were constructed using the IBM 3033 AP computer's VERSATEC plotter (Fig. 8 to 20). To create the surface contour maps a grid was constructed on a planar surface assigning the origin to the head of the Sur submarine canyon. Each data point was then assigned a cartesian coordinate on this grid based on its latitude and longitude /‾Ref. 83_7. Using this data the CONISD library subroutine from the W.R. Church Computer Center was able to construct surface contours of the indicated variable. Because of the low sampling density the hashed contours are at best a first approximation. The contour maps for chlorophyll a, nitrate, phosphate, and temperature extend further north than those which were constructed for ATP, GTP, and ATP/GTP because sampling for these variables continued from station 8 on the return transit to Monterey.

TABLE III

Biomass and Productivity Statistics

	High	Low	Mean	Standard Deviation	No. of Samples
ATP ($ng\ l^{-1}$)	3392	97	529	±520	57
CHLA ($mg\ m^{-3}$)	56	2	9	± 9	398
GTP (pM)	906	*	102	±135	57
GTP/ATP	.3	*	.1	± .1	51
Δ ATP/ATP	1.6	.1	.5	± .3	57

where * indicates that the values were below the level of detection

The two-dimensional surface spatial distribution of nitrate and phosphate relative to the California coastline is depicted in Fig. 8 and Fig. 9, respectively. The contour plots are constructed from data accumulated on 29 October 1980. The higher nutrient values and the sharpest temperature gradients were coincident (compare Fig. 8 and Fig. 9 with Fig. 10). Comparison of the surface temperature map (Fig. 10) with satellite IR imagery from the same day (Plate 1) reveals the strong thermal gradients located between the upwelling colder water along the periphery and the warmer oceanic water.

The ATP biomass shows several cells (Fig. 11). The highest concentration of biomass is located in the gradients at the equatorward edge of the feature. The level of ATP-biomass in this cell is approximately three times higher than that in either of the other two cells. The highest concentration of chlorophyll a biomass was found in the same geographical location (Fig. 12). The highest observed concentrations of both nitrate and phosphate were also located in this region (Fig. 8, 9), as was the highest level of GTP (Fig. 13). Although a relatively high level of protein synthesis was occurring in this area, the highest value of the productivity indicator, GTP/ATP, did not simultaneously occur at this location (Fig. 14).

The large standing crop observed adjacent to the strong chemical/thermal gradients of the upwelling feature supports the "natural chemostat" hypothesis which maintains

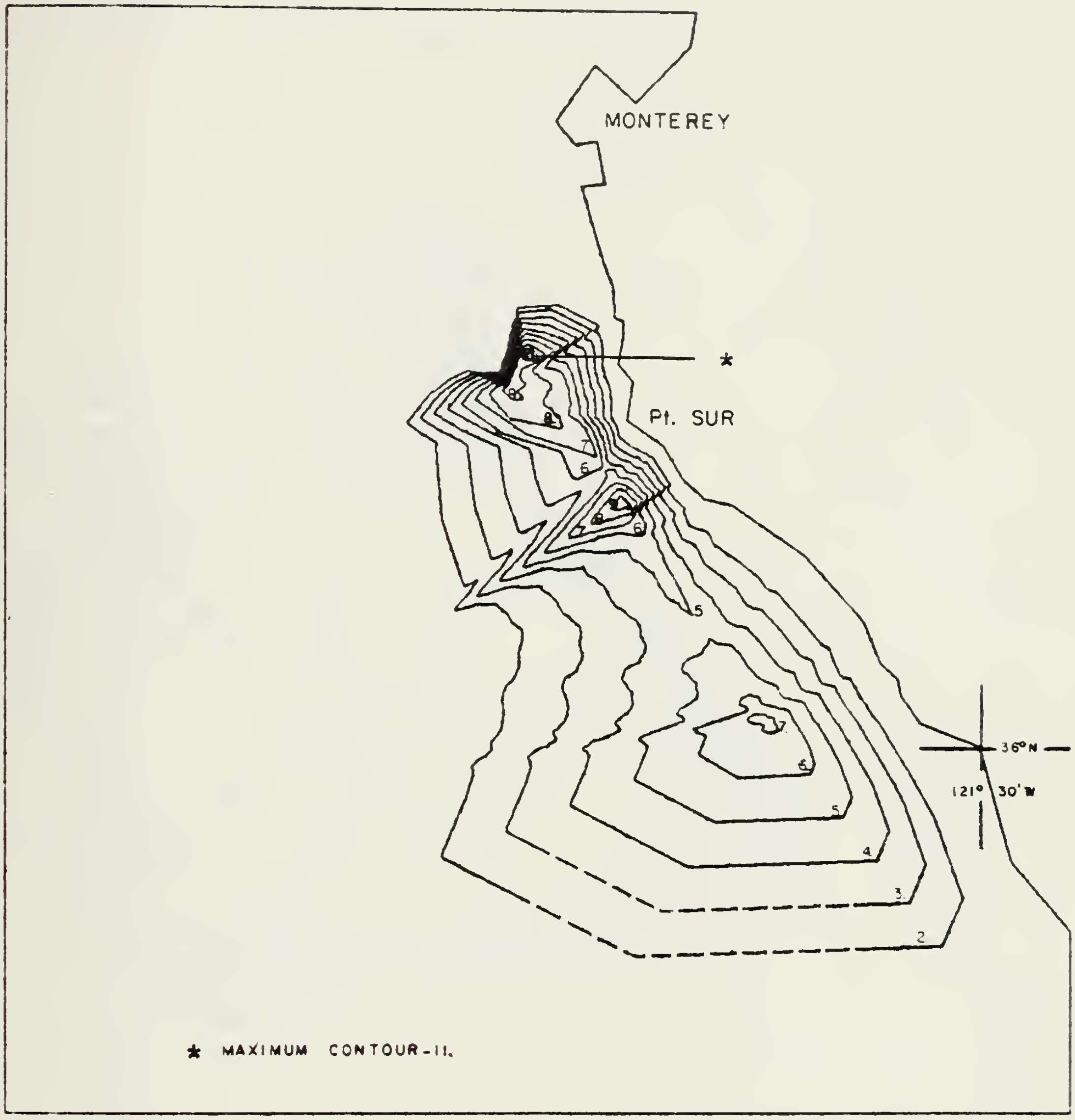

Figure 8. Surface Nitrate Distribution for 29 October 1980 Cruise data. Contour intervals of 1 µm.

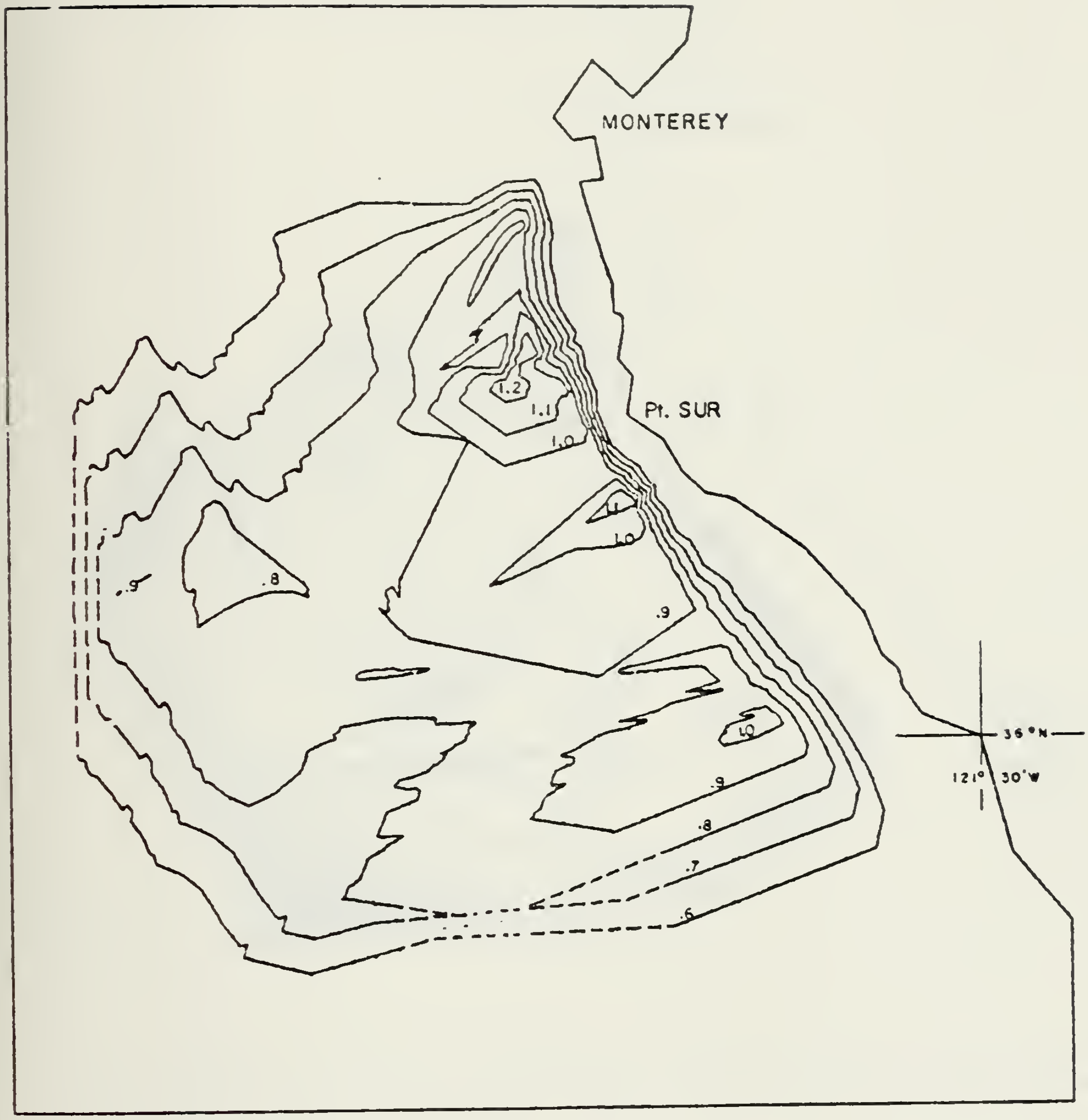

Figure 9. Surface Phosphate Distribution for 29 October 1980 Cruise Data. Contour intervals of .1 μM.

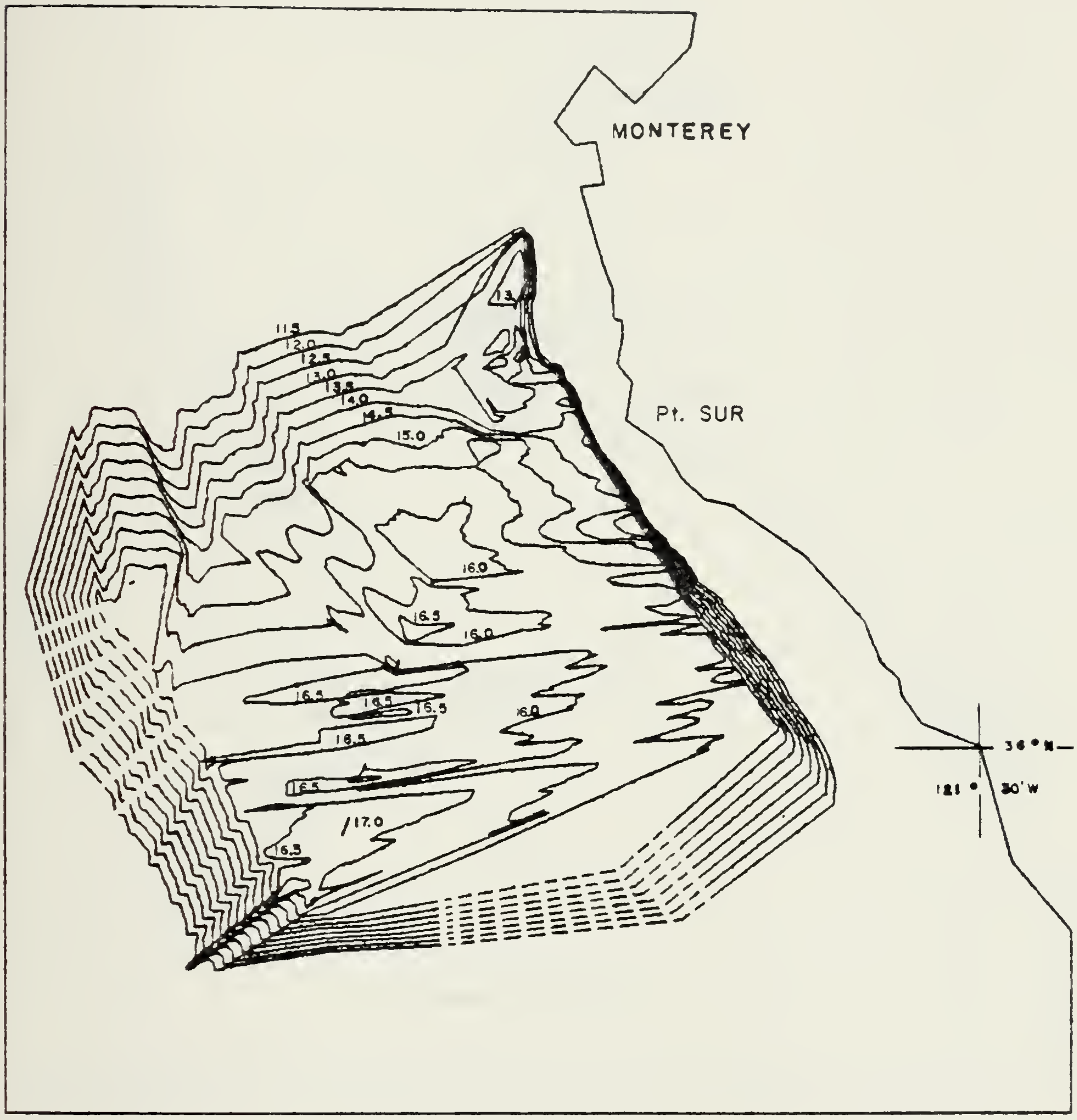

Figure 10. Sea Surface Temperature Distribution for 29 October 1980 Cruise Data. Contour intervals of .5°C.

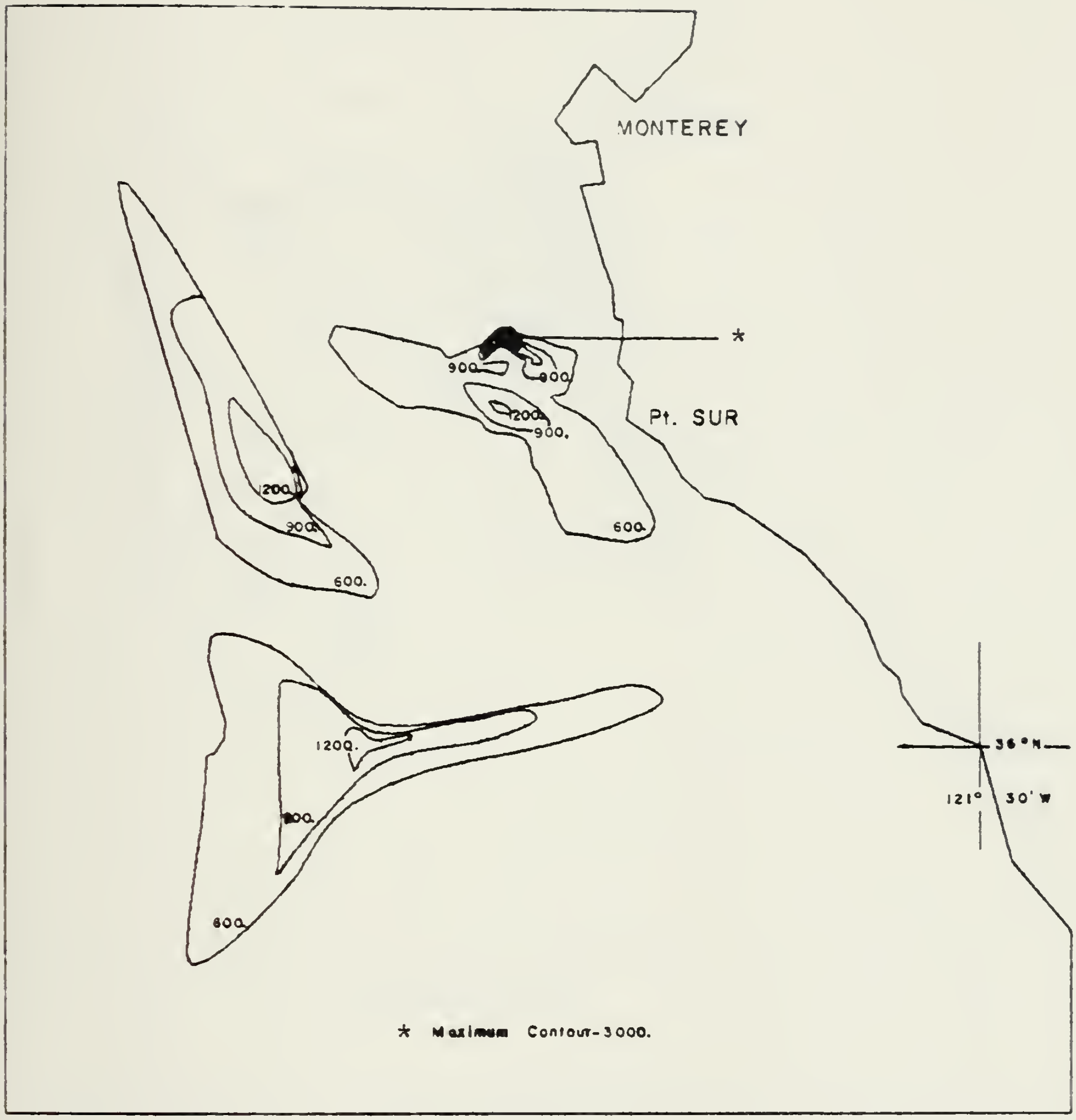

Figure 11. Surface Distribution of ATP for 29 October 1980 Cruise Data. Contour intervals of 300 ng l^{-1}.

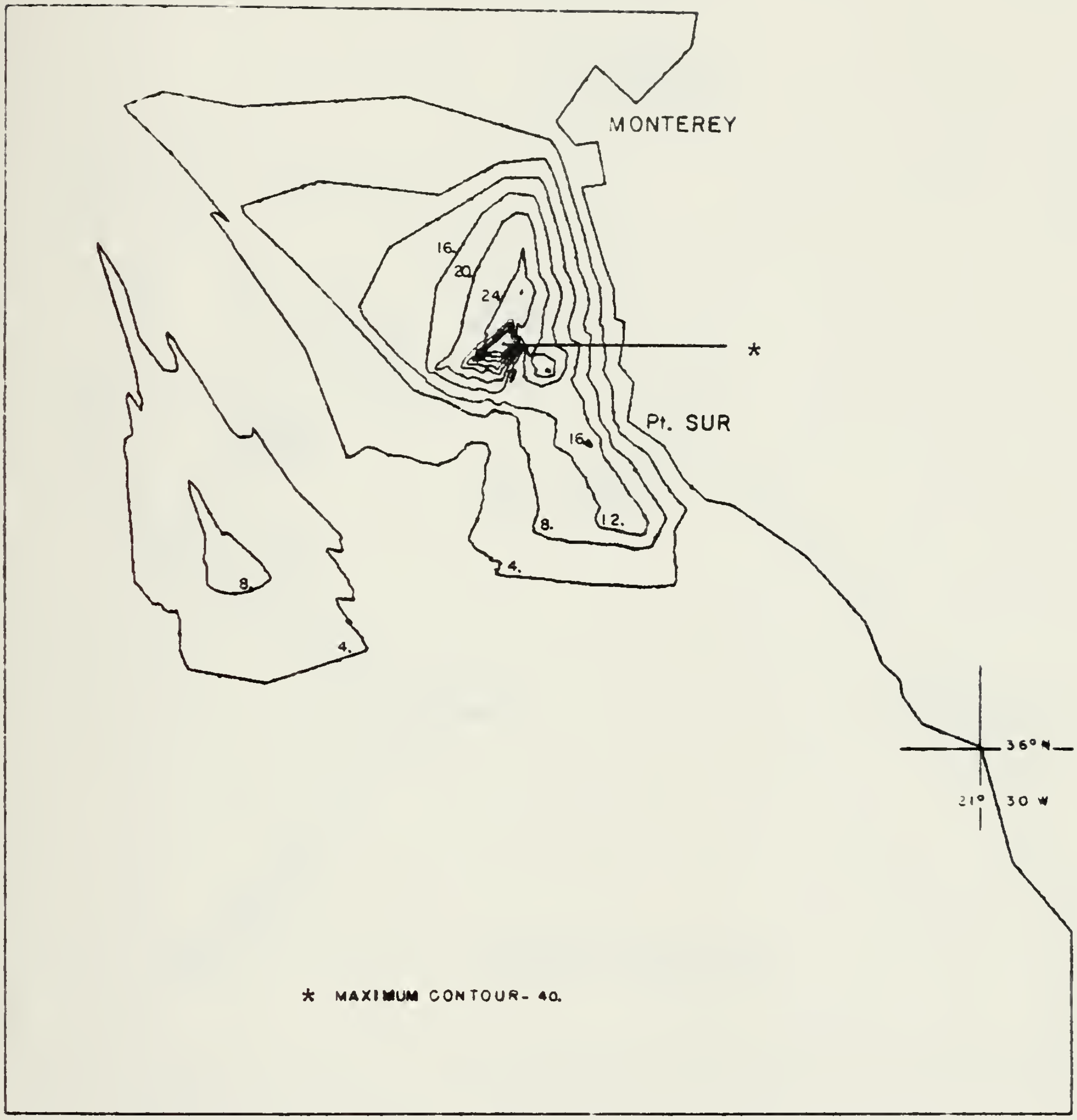

Figure 12. Surface Distribution of Chlorophyll a for 29 October 1980 Cruise Data. Contour intervals of 4 mg m^{-3}.

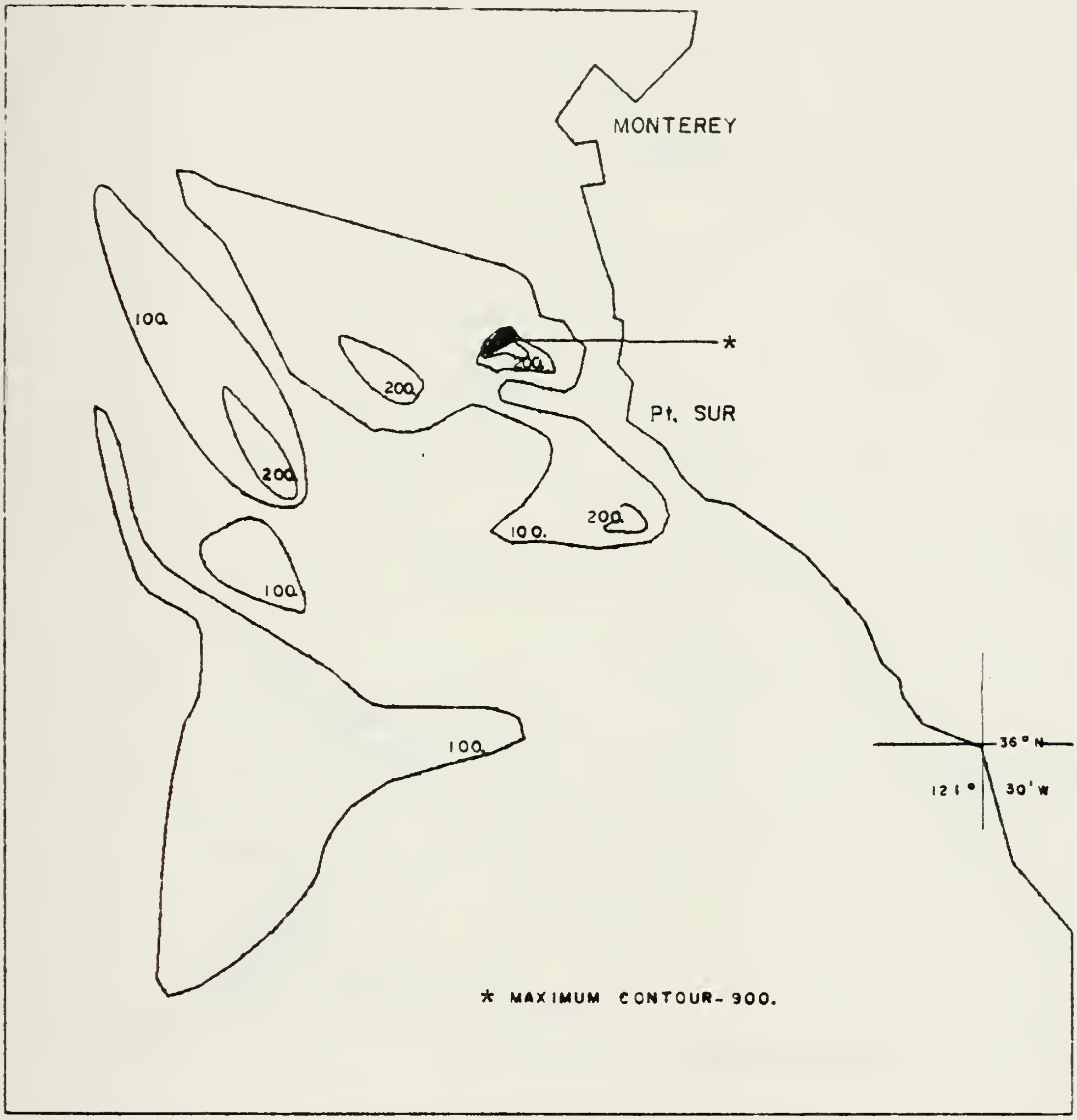

Figure 13. Surface Distribution of GTP for 29 October 1980 Cruise Data. Contour intervals of 100 picomoles l^{-1}.

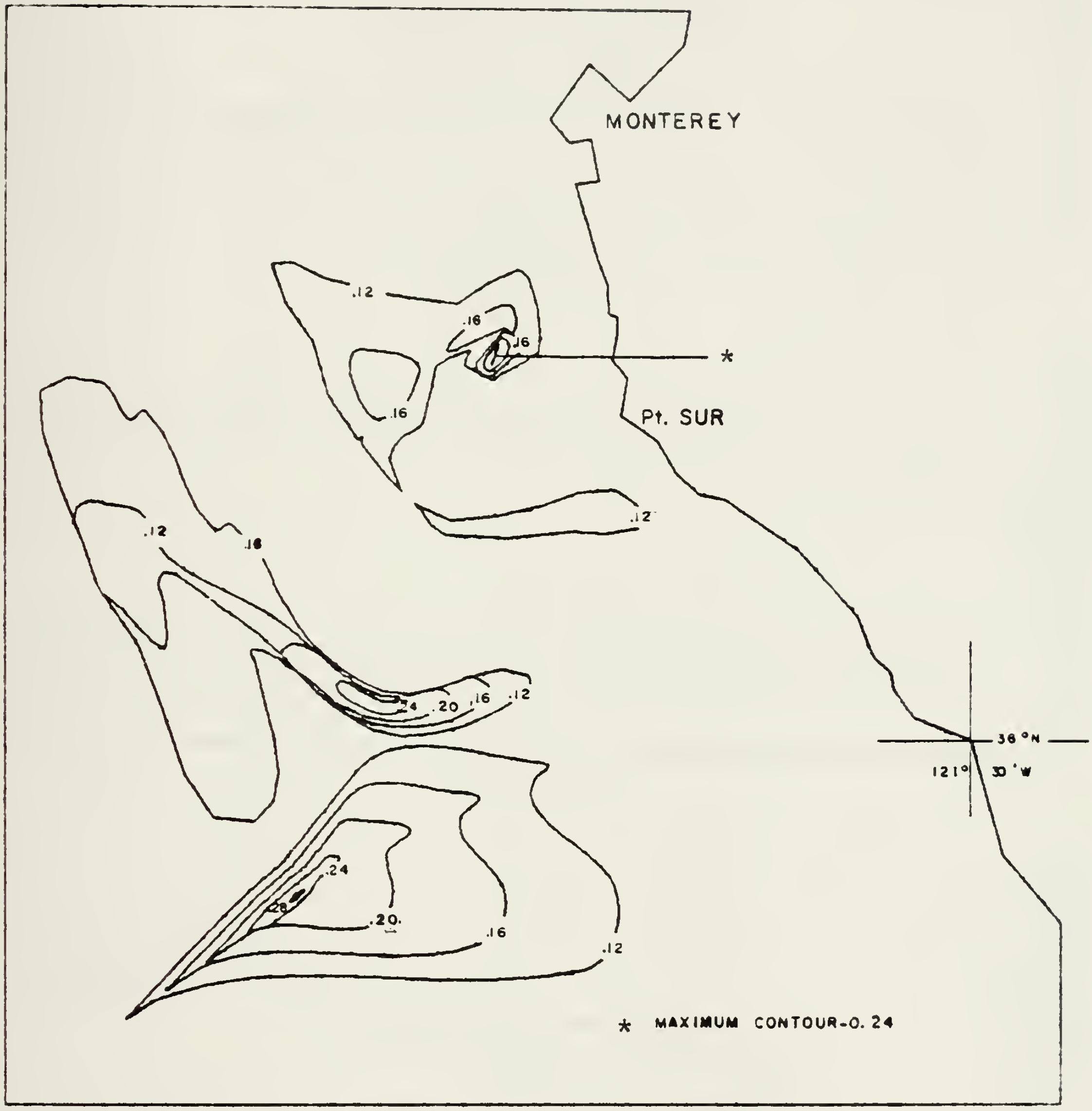

Figure 14. Surface Distribution of GTP/ATP for 29 October 1980 Cruise Data. Contour intervals of .04.

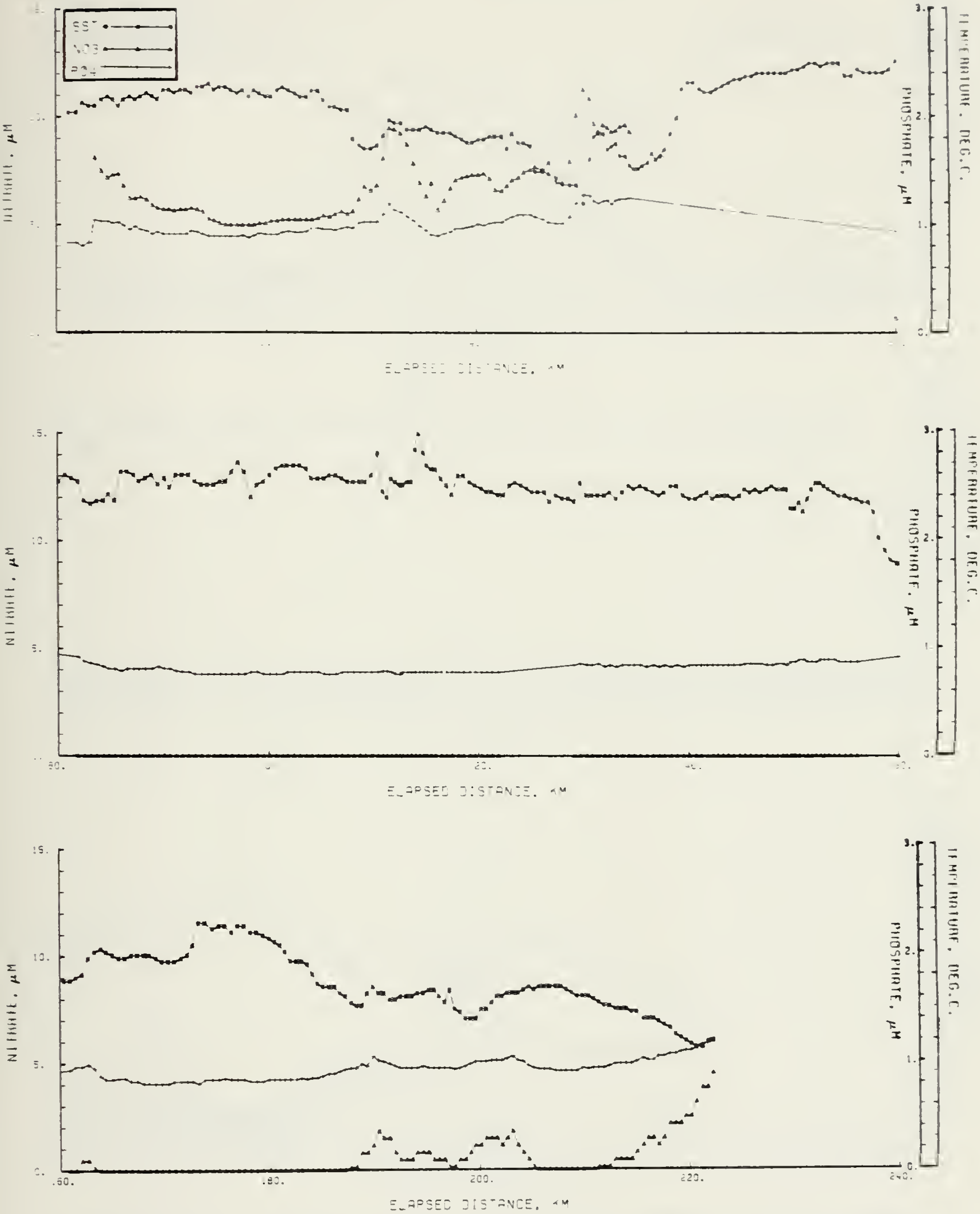

Figure 15. Nitrate, Phosphate, and temperature versus elapsed distance along the 29 October 1980 cruise track.

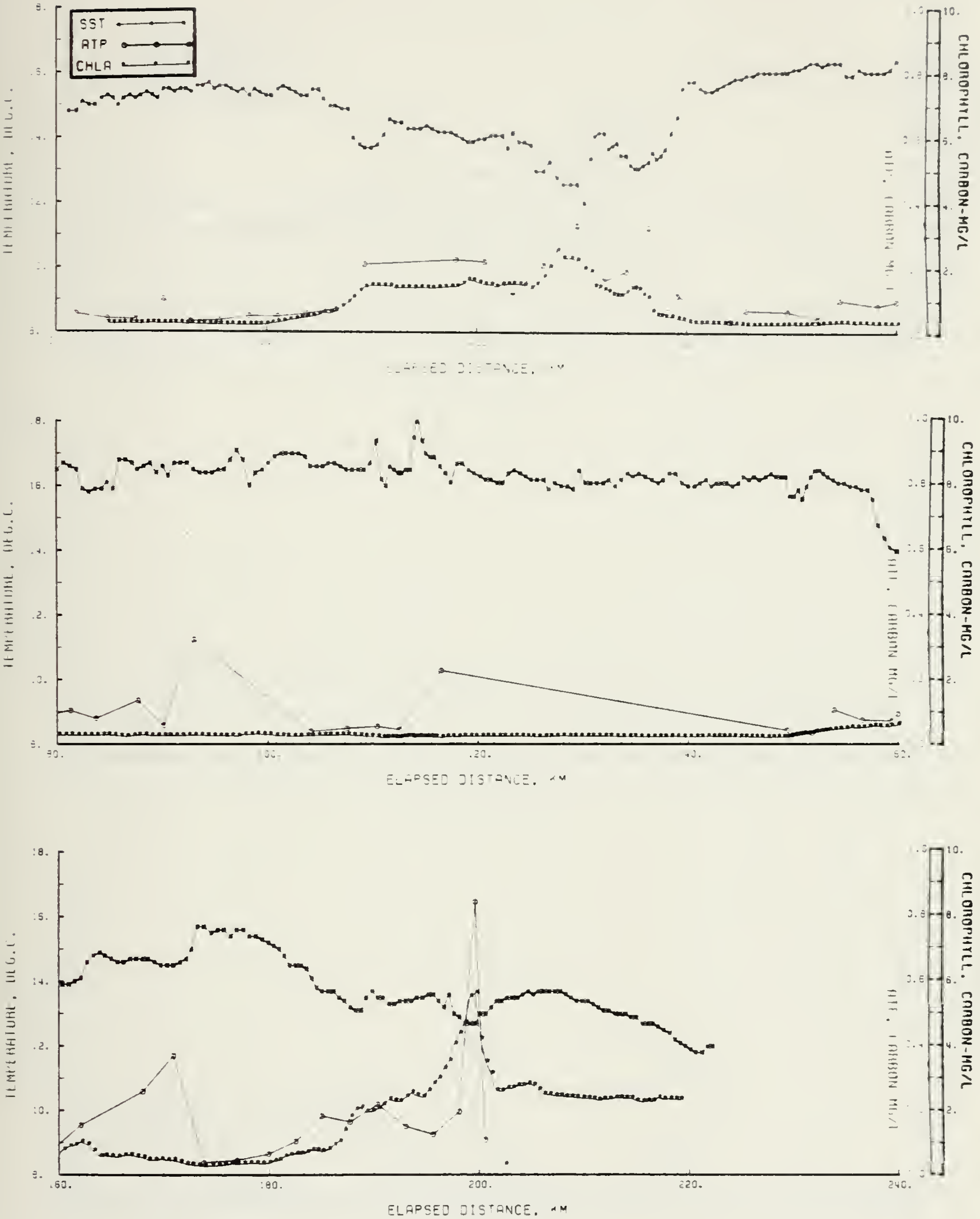

Figure 16. Chlorophyll a, ATP, and temperature versus elapsed distance along the 29 October 1980 cruise track.

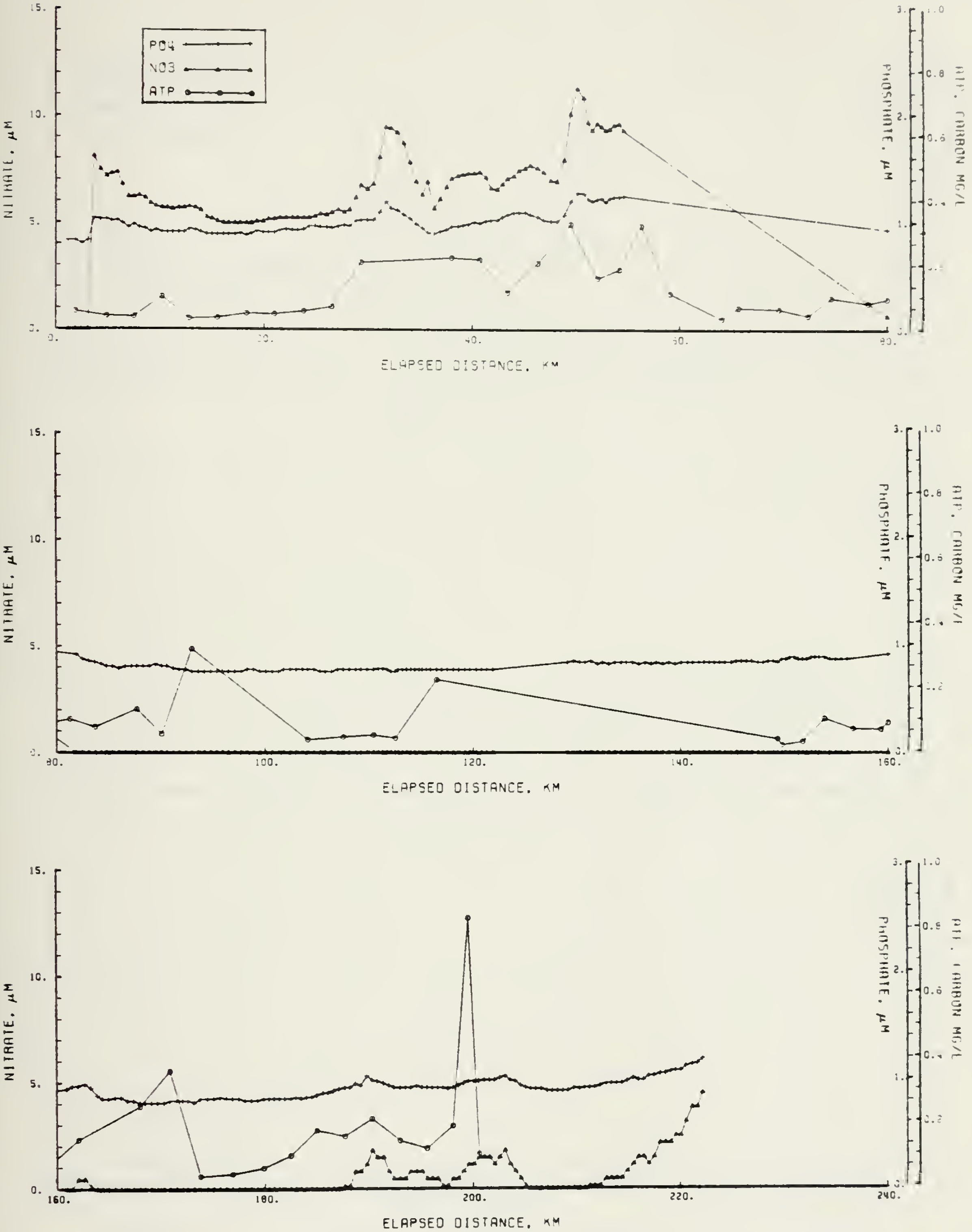

Figure 17. ATP, Nitrate, and Phosphate versus elapsed distance along the 29 October 1980 cruise track.

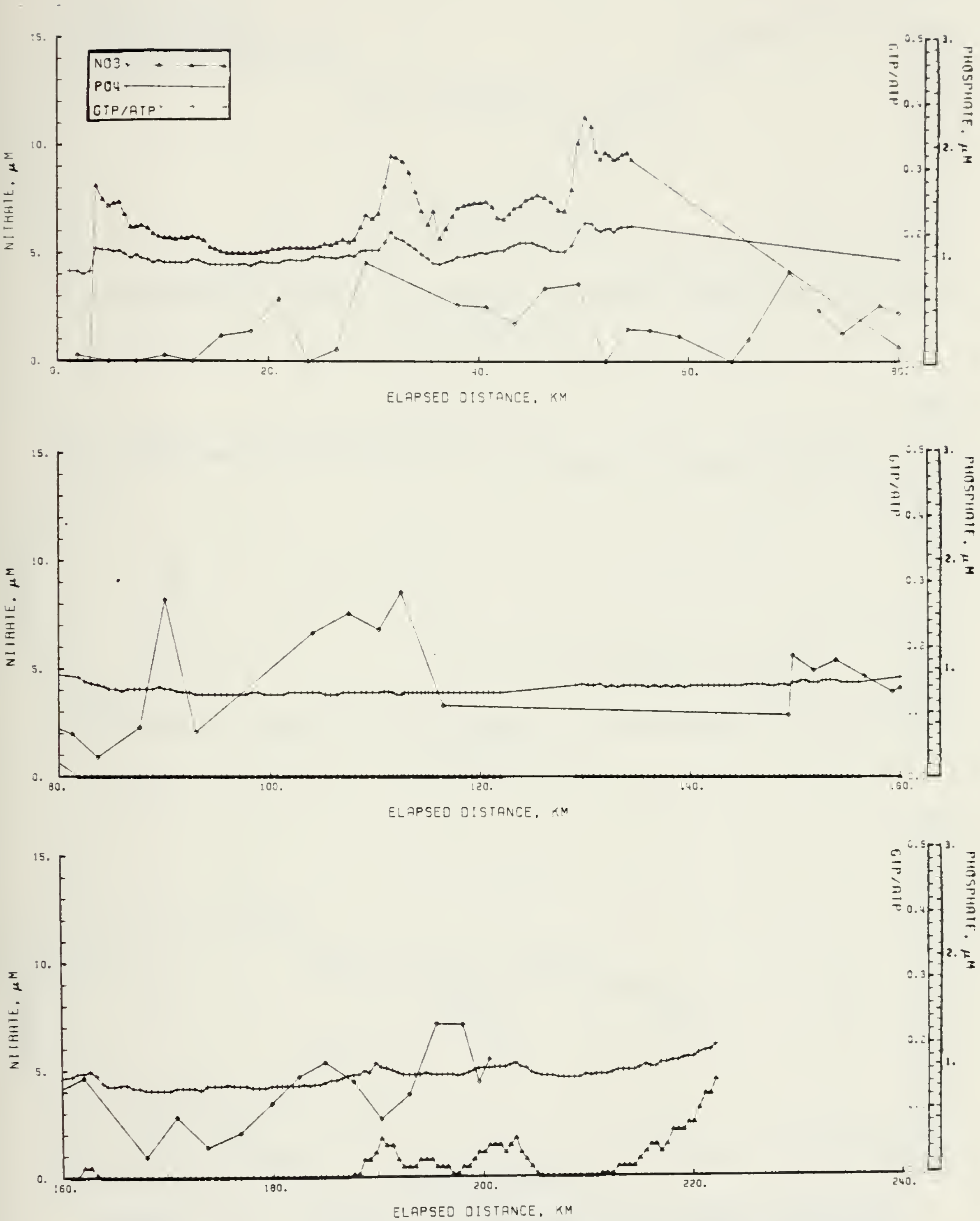

Figure 18. GTP/ATP, Nitrate, and Phosphate versus elapsed distance along the 29 October 1980 cruise track.

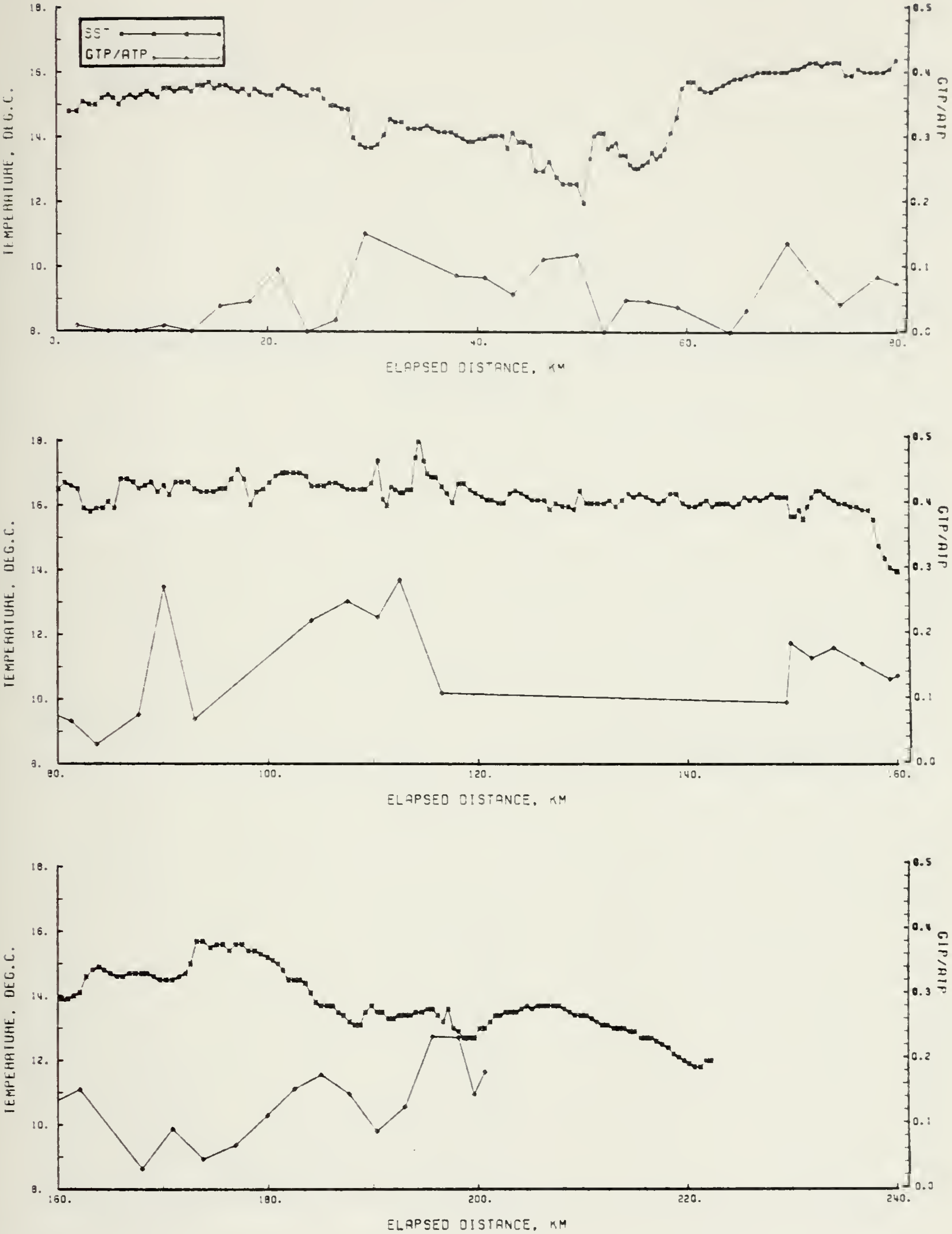

Figure 19. GTP/ATP and Temperature versus elapsed distance along the 29 October 1980 cruise track.

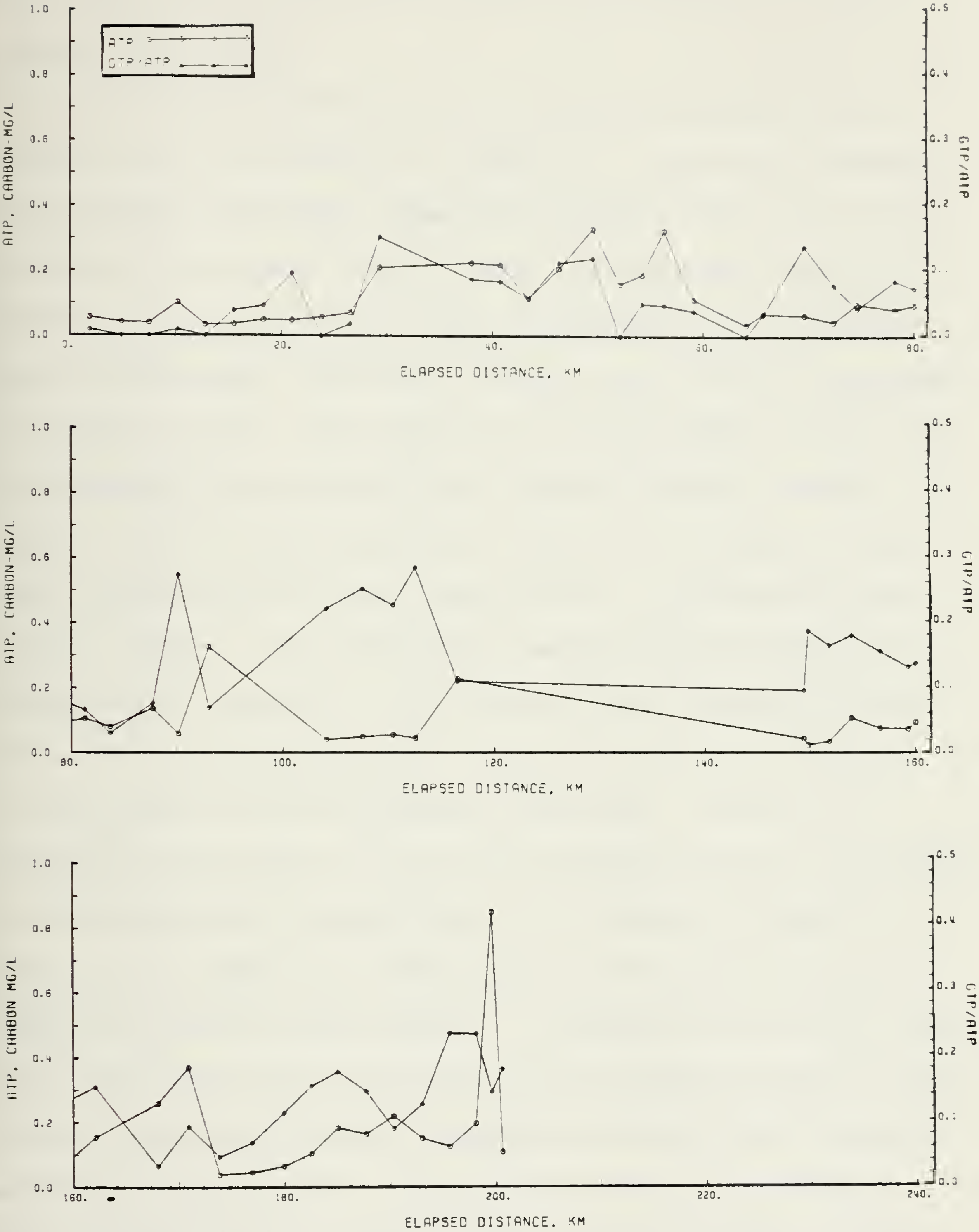

Figure 20. GTP/ATP and ATP versus elapsed distance along the 29 October 1980 cruise track.

that conditions for optimal growth are produced in these regions /‾Ref. 84_7.

Correlation coefficients for various parameters were computed and are summaried in Table IV. Since the correlations between variables depend not only on the initial conditions of the source water, which evolves over time as a result of both conservative and nonconservative processes such as advection, diffusion, mixing, heat and salt transfer, biological uptake, and release of nutrients /‾Ref. 85_7, the instantaneous relationships are complex and the instantaneous chemical and biological status of a feature is not easily deduced from point observations. Correlations are useful, however, for determining general relationships and trends among variables. The correlations indicated under the column "all data points" contain correlations between all the points of the indicated variables. Values of variables which were too low to be detected were not included in the correlation calculations. An attempt was made to obtain more insight by subdividing the data into two groups based on nitrate concentrations. Figures 21 and 22 are point plots which show the dissolved nitrate concentrations plotted against those of dissolved phosphate concentration and temperature, respectively. These figures depict the separation between the two distinct water masses present. Figure 23 is a point plot of dissolved phosphate versus temperature This figure does not similarly show a distinct separation.

TABLE IV

Correlation of Nutrients, Temperature, and Biomass Indicators

	All Data Points	New Water	Old Water
ATP:CHLA	.67	.94	.62
ATP:GTP	.88	.91	.91
CHLA:GTP	.79	.85	.78
GTP/ATP:ATP	-.05	.65	-.16
GTP/ATP:GTP	.32	.86	.18
GTP/ATP:CHLA	.24	.65	.17
ATP:TEMP	-.54	-.93	-.47
CHLA:TEMP	-.82	-.94	-.85
GTP:TEMP	-.52	-.86	-.54
GTP/ATP:TEMP	.02	-.66	.05
NO3:TEMP	-.58	-.21	-.78
PO4:TEMP	-.77	-.70	-.86
NO3:ATP	-.15	.77	.25
NO3:GTP	-.31	.69	.12
NO3:CHLA	-.54	.40	.06
NO3:GTP/ATP	-.59	.41	-.43
NO3:PO4	.43	.55	.82
PO4:ATP	.26	.65	.34
PO4:GTP	.28	.58	.47
PO4:CHLA	.58	.62	.80
PO4:GTP/ATP	-.18	.36	.02

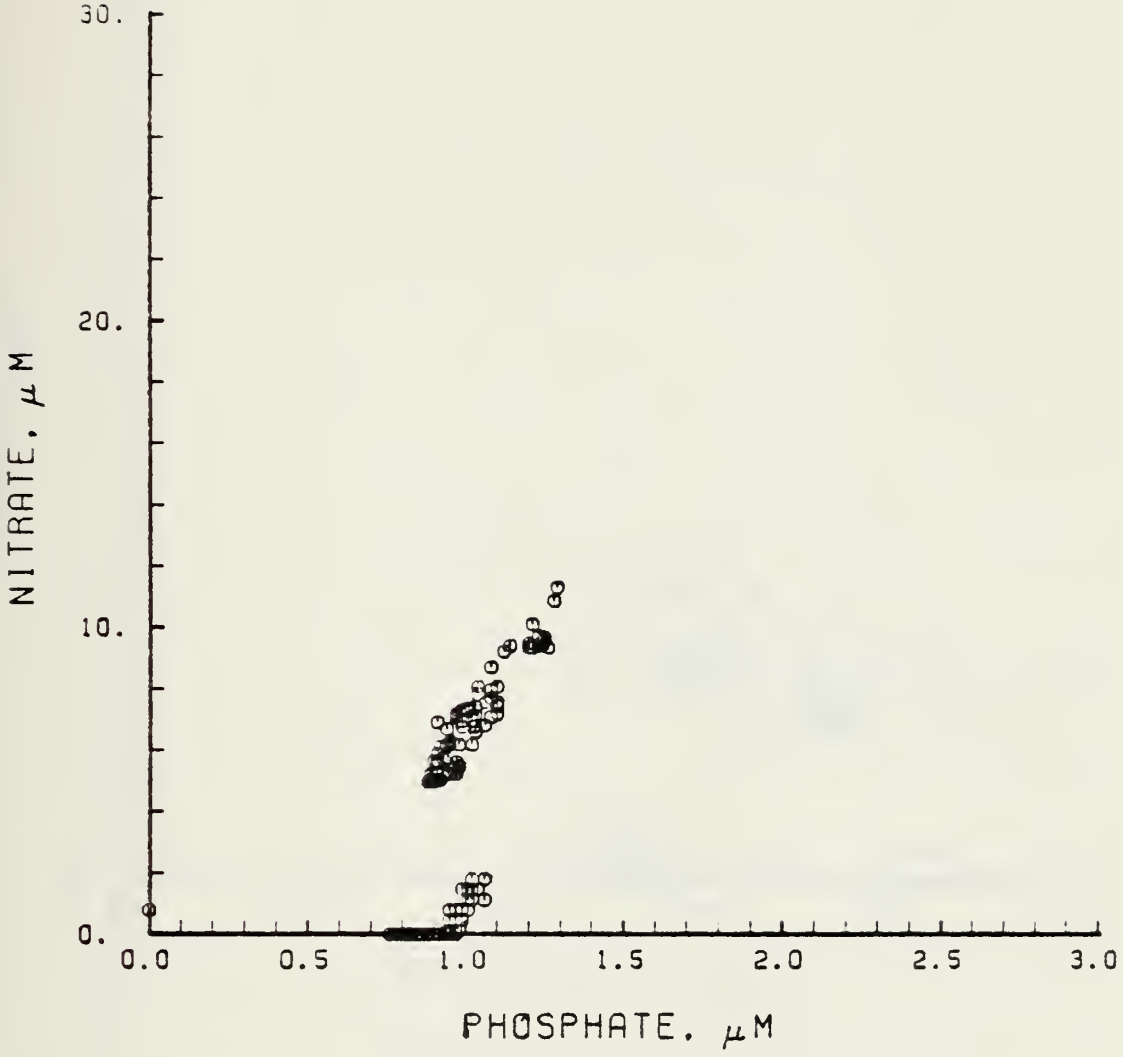

Figure 21. Nitrate versus Phosphate for 29 October 1980 cruise data.

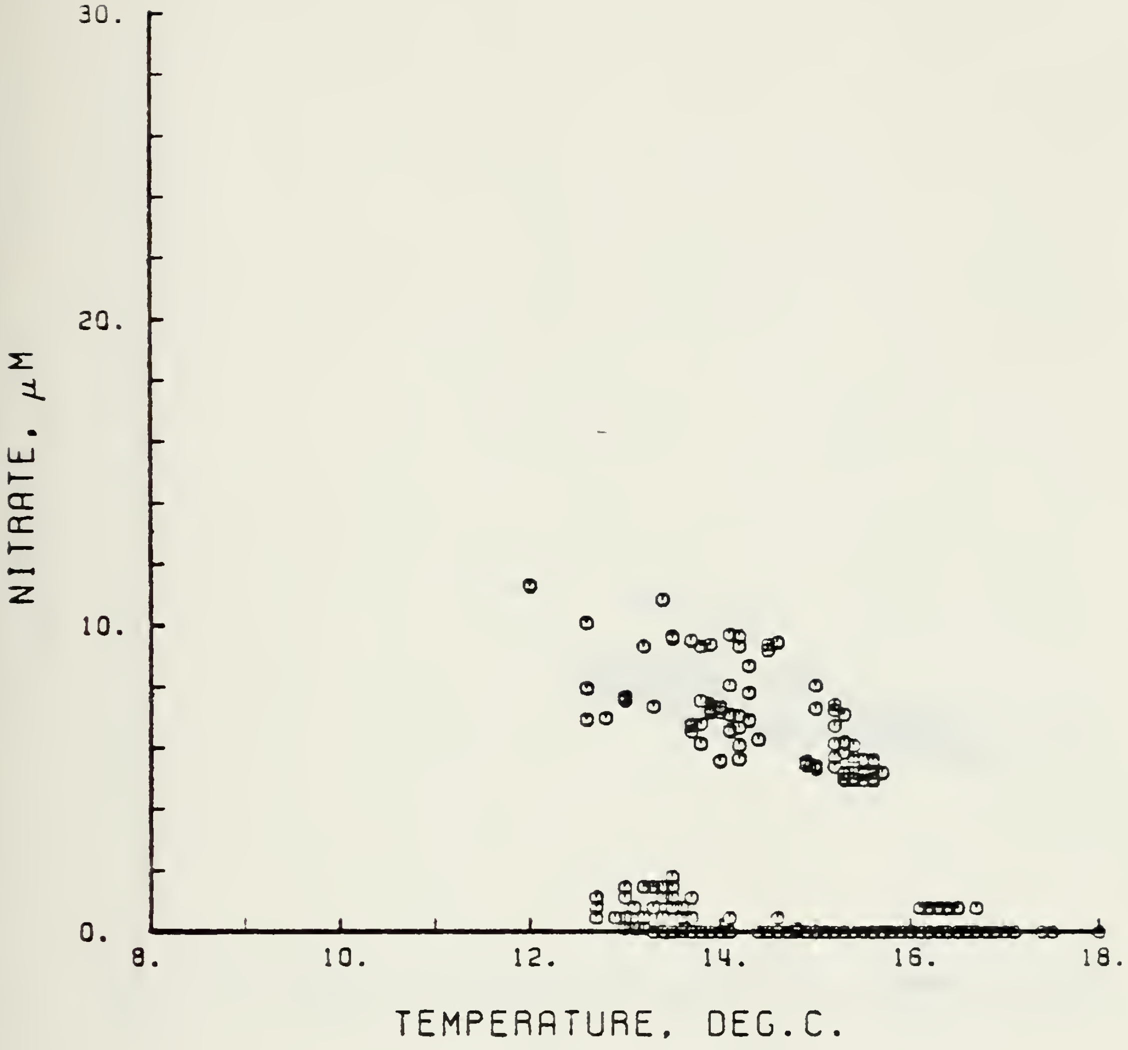

Figure 22. Nitrate versus Temperature for 29 October 1980 cruise data.

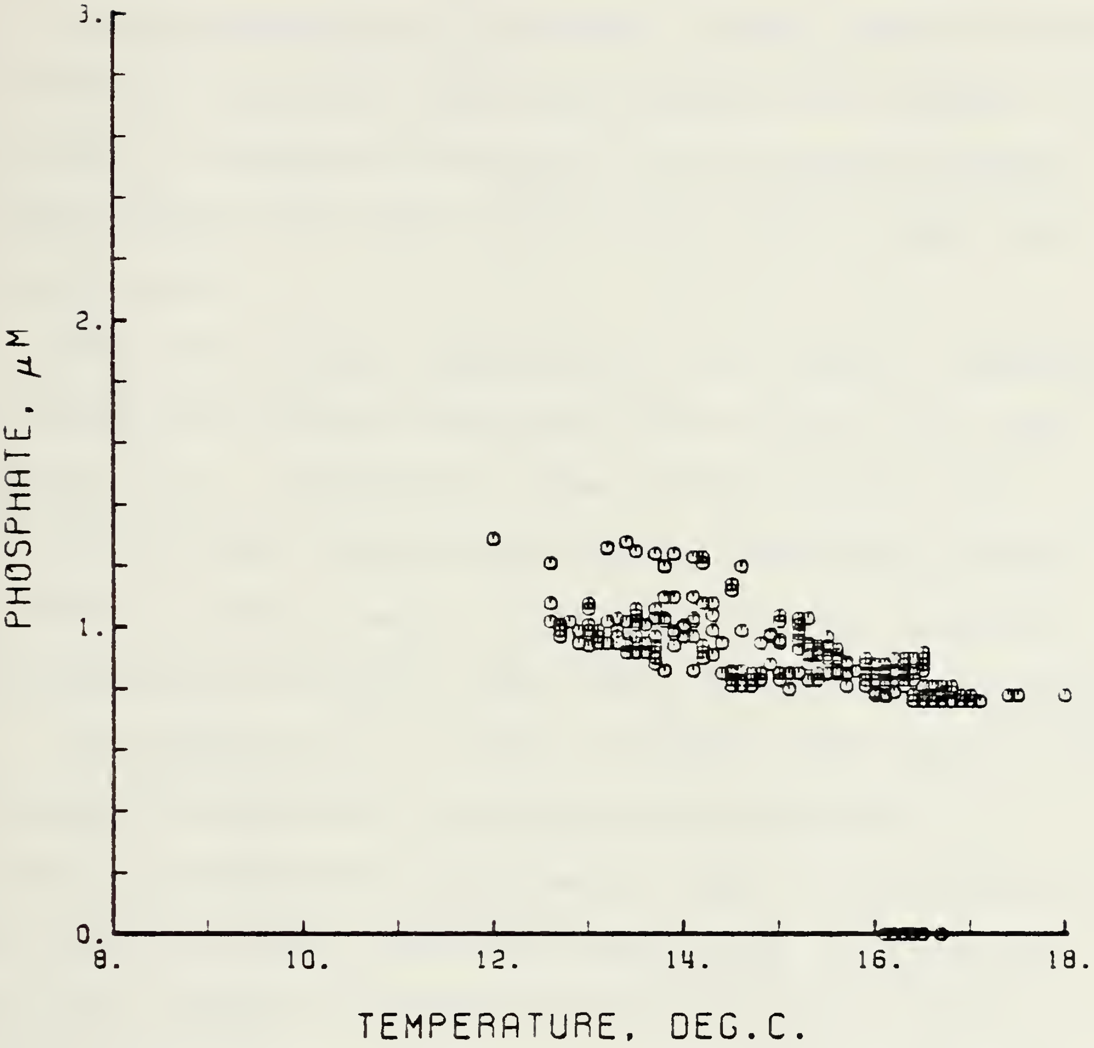

Figure 23. Phosphate versus Temperature for 29 October 1980 cruise data.

Based on this separation an arbitrary value of 2.0 μM was used as the dividing mark to separate the values. Water which contained dissolved nitrate in excess of 2.0 μM was designated as "New Water." These higher nutrient values were observed along the transect from station 9 to 8 (Fig. 2) during the first 55.0 km of elapsed distance. Values during this part of the cruise track ranged from 5 to 11 μM.

The second group, designated as "Old Water," consisted of data points whose dissolved nitrate content was less than 2.0 μM. Essentially these values occurred over the rest of the cruise track (Fig. 2) beginning halfway between stations 8 and 6, to station 7, until station 8 was approached where the "New Water" was encountered again.

From 55.0 to 81.3; 122.4 to 128.6; 156.6 to 160.4 km elapsed distance the autoanalyzer was inoperative so nitrate and phosphate measurements could not be made and the water at these locations could not be classified as to type. Values for these and other variables which were correlated under the subcategories of "New Water" and "Old Water" were not included from these portions of the cruise track.

In some places where the correlations do not show internal consistancy, more points were correlated under the "all data" point category than under the "New" and "Old Water" mass combined categories. Data which could

not be placed in either subcategory were not included in the "old" and "new" categories even though they were correlated when all data values were considered.

B. RESULTS OF THE CARBON-14 UPTAKE EXPERIMENT

Table V contains the results from the ^{14}C uptake-productivity experiment. Results listed are the average values determined from duplicate subsamples which were analyzed in tandem. The GTP and ATP concentrations used to determine the productivity ratio were analyzed from subsamples of the light bottles.

TABLE V

C-14 Uptake Results

Sample	CHLA (mg m^{-3})	^{14}C Uptake (mgC m^{-3} h^{-1})	Assimilation Number (mgC mgChla^{-1} h^{-1})	GTP (Pm)	GTP/ATP
#1	21.53	31.9	1.48	134.5	.178
#2	7.75	22.9	2.95	152.5	.178
#3	43.06	25.9	.60	112.9	.110
#4	3.44	.58	.17	69.4	.103
#5	2.36	.59	.25	60.4	.110

Table VI illustrates the results of correlation calculations between the specific productivity indicators, assimilation numbers and GTP/ATP ratios, and absolute productivity indicators, ^{14}C uptake and GTP. Correlation

TABLE VI

Correlation of Productivity Indicators

	Assimilation #: GTP/ATP	^{14}C Uptake: GTP
All Data Samples	.89	.89
Sample #1 Removed	.99	.88
Sample #2 Removed	.96	.99
Sample #3 Removed	.89	.92
Sample #4 Removed	.86	.85
Sample #5 Removed	.87	.82

statistics were first determined for all samples and then successively with the values of each sample removed in turn from the data set to determine if deletion of one sample from the data set would significantly alter the correlation statistics.

C. RESULTS OF THE TIGRIOPUS CALIFORNICUS PRODUCTIVITY EXPERIMENT

Table VII contains the results of the productivity determinations for different population groupings of Tigriopus californicus. Specific productivity, GTP/ATP, is compared to the RNA/DNA ratio determined by Baugh for similar population subgroups of Tigriopus californicus.

TABLE VII

Relative Rates of Productivity for *Tigriopus californicus*

	GTP/ATP	RNA/DNA (from Baugh [Ref. 85])
Gravid	.125	4.62
All-But-Gravid	.099	2.16
Mixed	.189	3.15

IV. DISCUSSION

A. OCTOBER 1980 CRUISE

A quasisynoptic approach based on point sampling was used to study the spatial heterogeneity and productivity of biomass. An assumption made when obtaining point samples is that they are representative quantitatively of population and community parameters in the body of water sampled. One study which has examined this problem found that precision was not increased merely by increasing the sample volume [Ref. 87]. Generally the precision is only increased when the patch size increases so that the probability of sampling the "right" number of patches and of capturing the "correct" number and kinds of individual organisms representative of the general area is increased. This is one of the problems associated with discrete sampling methods for ATP and GTP.

Another problem is encountered when point data collected over an extended time period is used to characterize the biology and productivity of an entire area, since these variables are continuously in flux changing spatially and temporally even as the measurements are made. A study, which looked at the variability in the spatial and temporal heterogeneity of phytoplankton biomass in relation to the horizontal spatial structure of physical and chemical

variables in surface waters [Ref. 88], found that the time component contributed to 63 percent of the total variance in the data, while the contribution of the space component was only 3.5 percent. The time component included the daily changes in available insolation and water column variables. Another study [Ref. 89] similarly found that rapid temporal variations could occur over a time period of a few days which produced variations in chlorophyll concentration ranging 21 to 45 percent and variations in phosphate concentration ranging from 32 to 64 percent. Similar fluctuations could be expected for ATP and GTP determinations.

Although at any moment there exists specific relationships between the different variables observed in the environment, data from the October cruise suggest that these interactions are continuously and rapidly changing and that the spatial distribution of phytoplankton is successively controlled by different factors or by a complex state of equilibrium between these variables.

One temporal variation which is difficult to take into account is the diel depth variation which occurs. A possible way to circumvent this difficulty in future experiments would be to pump water from the chlorophyll maximum instead of from the depth of the ship's intake using a depth variable fluorometer.

Figure 15 graphically illustrates the relationship between some of the physical and chemical variables of this system. The most significant correlations for these variables occur in the "Old Water" where nitrate and phosphate are highly positively correlated and nitrate to temperature and phosphate to temperature are highly negatively correlated. The high correlation between nitrate and phosphate is due to the uniformly low values of both which are observed in the "Old Water." The high inverse correlation between the temperature and the nutrients indicates, in view of the relatively high temperature values and low nutrient concentrations, that this water has been substantially altered from its initial condition through dynamical and biological processes. The correlations for "all data" points and for the "New Water" indicate substantially the same result, although in these categories it is apparent through the lower correlation coefficients.

The highest values of nitrate and phosphate, 11.35 μM and 1.29 μM respectively, were observed in the gradients at the southern edge of the upwelling feature where the nitrate to phosphate ratio was 8.8 to 1. Since phytoplankton uptake nitrate and phosphate in a ratio of 16 to 1 /‾Ref. 90_7, the relationship between the nutrients suggests that the water masses observed are or will be nitrate limited. Since the steady state biomass is regulated by the concentration of the limiting nutrient

in the aquatic environment, it is important to identify this critical element to understand the dynamic relationship between chemical mesoscale and biological patchiness [Ref. 91]. Studies have provided evidence that the nutrient and light requirements of phytoplankton follow a pattern similar to the Michaelis-Menten hyperbolic relationship for enzyme kinetics [Ref. 92, 93, 94, 95, 96, 97]. Results of MacIsaac and Dugdale [Ref. 98] have shown that nitrate uptake by phytoplankton will generally increase with nitrate concentration only up to nitrate levels of about four μM at which time any excess in the environment is superfluous. It is apparent that phytoplankton in the "New Water" have sufficient nitrate available to provide optimal nutrient conditions necessary for maximal growth. This state contrasts to that in the "Old Water" where the availability of nitrate falls below detectable limits along large stretches of the cruise track. When the data were divided into two groups based upon their dissolved nitrate concentration, some interesting results emerged.

Table III contains the range of values for the biomass and productivity parameters over the area surveyed (Fig. 2). There was a great deal of variability in the data due to the juxtaposition of adjacent water types. Table VIII illustrates the average GTP, ATP, and GTP/ATP levels taken from studies of various water masses at varying depths.

According to Karl [Ref. 100] typical surface ATP concentrations range from greater than 500 ng l^{-1} for

TABLE VIII

GTP/ATP Ratios in Environmental Samples
(adapted from Karl [Ref. 99])

	Concn[a]		
Sample Description	GTP[c]	ATP	GTP/ATP
Southern California seawater (32° 43.2' N, 117°30.1'W)[b]			
10 m, total	55.7	312	0.18
10 m, $<10\ \mu m$	21.8	58	0.32
100 m, total	31.2	22	0.14
100 m, $<10\ \mu m$	6.3	16.5	0.38
500 m, total	2.5	11.8	0.22
500 m, $<10\ \mu m$	1.9	4.5	0.42
Southern California seawater (33° 30.1' N, 119°20.0'W)			
5 m	82	550	0.15
50 m	68	523	0.13
200 m	8.5	65	0.13
500 m	5.0	26	0.19
1000 m	2.6	20	0.13
1550 m	2.5	20.8	0.12
Black Sea seawater (42°50.0' N, 33° 00.0'E)			
10 m	68	462	0.15
75 m	12.7	89	0.14
123 m	16.6	41.4	0.40
195 m	14.6	35.3	0.41
489 m	3.6	9.1	0.40
974 m	3.0	12.0	0.25
1992 m	6.4	26.2	0.24
Galapagos Rift seawater (00° 47.0'N, 86°08'W)			
50 m	46	286	0.16
500 m	<0.6	8	<0.075
Hydrothermal vents (2,500m)	832	968	0.86
Catalina Island (Calif.) sediments (33°21'N, 118°30' W), low tide			
0-1 cm	620	892	0.70
5 cm	96	93	1.03
10 cm	38	24	1.58
Ocean Beach (Calif.) sediments (32°45'N, 117°16'W), low tide			
0-1 cm	208	355	0.59
5 cm	247	359	0.69
10 cm	142	187	0.76

---

[a] GTP and ATP concentrations are expressed as picomoles per liter for seawaters, and picomoles per cm^3 for sediments.

[b] Total, seawater filtered onto a Reeve Angel 984-H filter disk; $<10\ \mu m$, 10-μm Nitex filtrate filtered onto a Reeve Angel 984-H filter disk.

[c] [GTP] = [GTP + uridine 5'-triphosphate] x 0.53 .

productive eutrophic waters to 100-500 ng l^{-1} for relatively barren regions of the ocean. The area surveyed ranges between extremes of 96.7 ng l^{-1} to 3391.8 ng l^{-1} indicating considerable variability between point measurements. As evident in Table III, the mean ATP level of 529.1 ng l^{-1} indicates that on the average the surface layer of this region contained a large amount of biomass. This largest concentration of ATP-biomass is located in the colder water as indicated by the high negative correlations between ATP and temperature.

The overall values for chlorophyll a were quite high, ranging from a low of 2.0 mg m^{-3} to a high of 56.4 mg m^{-3} with an average value of 8.7 mg m^{-3}. The highest amount of chlorophyll a-biomass was found in the colder nutrient rich water as indicated by the high negative correlation between chlorophyll a and temperature, and high positive correlations between chlorophyll and both nitrate and phosphate.

When these values were converted to units of carbon and compared to the ATP values which had been converted to equivalent units of carbon, the chlorophyll a values indicated that about seven times more biomass was present than indicated by the ATP values. Several factors could account for this disparity. The difference in measured levels could be due to sampling technique, as suggested by Bronsink /‾Ref. 101_7. Since the ATP water samples are prefiltered and the flow of water to the fluorometer is not,

the disparity could be caused by the exclusion of phytoplankton larger than 200 microns from the sample. Alternatively, filtration could cause stress which lowers ATP levels. Or, the ratio converting chlorophyll *a* to carbon may be significantly less than the factor, 100, which was the value used in the data reduction for this study. Steele and Baird determined that the conversion factor for chlorophyll *a* to carbon ranged in their study area from 30 to 100 [Ref. 102]. Eppley has proposed a conversion factor of 54 ± 17 [Ref. 103]. Use of a lower conversion factor would bring the relative amounts of biomass as measured by ATP into closer agreement with the value determined by chlorophyll *a*. Chlorophyll *a* variations have been explained as a result of the reaction of phytoplankton to limitations in the environment. It has been shown [Ref. 104] that the size of the photosynthetic unit, and correspondingly the amount of chlorophyll *a* present within most species of phytoplankton observed will increase in response to low light intensities. If this were the case in dense plankton blooms the concentration of chlorophyll *a* would be inflated in relation to the amount of biomass actually present in the environment. In support of this is a study which shows that fluorescence varies two to five times when phytoplankton are exposed to varying conditions in the environment [Ref. 105]. Nevertheless, since the correlations between ATP and

chlorophyll a are significant (refer to Table IV) for all data points and subsets thereof, confidence can be placed in the relative relationships of biomass present along the cruise track.

Figures 11 and 12 show the 2-dimensional spatial distribution of these biomass indicators. Of particular interest is the biomass peak which is located in northeast corner of these figures. Comparison with Figures 8, 9, and 10 clearly show that this very high concentration of biomass occurs in the strong chemical and thermal gradients located at the southern edge of the upwelling feature. This peak in biomass is roughly three times greater than that indicated in either of the other two cells in Figure 11. The biomass concentration observed in the chlorophyll distribution at this same location is roughly seven times greater than that observed in the second chlorophyll a cell (Fig. 12). Figure 16 graphically illustrates the correlation of these two biomass indicators along the cruise track. Of special interest are the peaks of biomass which occur in the temperature gradients. Figure 17 graphically depicts the relationship between the biomass, indicated by ATP levels, and the distribution of dissolved nutrients, nitrate and phosphate. The nitrate and phosphate values are highly correlated to the ATP values (refer to Table IV) within the "New Water." In this first section of the cruise track the biomass peaks appear to mirror those of

the nutrients, being slightly skewed toward the gradients. The higher correlation between biomass and nutrients in the "New Water" indicates that the higher the nutrient concentration the higher the biomass will be. Inversely, the higher the biomass the more nutrients are utilized and depleted, hence the lower correlation coefficients which were computed for these parameters in the "Old Water." These findings support the "natural chemostat" hypothesis [Ref. 106] which observes that the "steady state biomass is proportional to the concentration of added limiting nutrient" [Ref. 107].

Of particular interest are the high nitrate and biomass concentrations at approximately 50.0 km elapsed distance. This point is geographically located approximately at station 8 (Fig. 2). About two hours later this station was approached again at an elapsed distance of 198.6 km. At this time, the nitrate levels had fallen significantly, phosphate levels had decreased slightly, and the highest level of biomass observed during the cruise was encountered. Although it is unlikely that the same location was sampled, since the maximum growth rate for phytoplankton is approximately one doubling per day [Ref. 108], a strong possibility does exist that it is part of the same patch, since patch sizes are generally 5-10 km in diameter [Ref. 109]. Data from studies conducted in the Peruvian upwelling system indicates that productivity is three times higher on the periphery of a patch than at its center [Ref. 110, 111,

112]. Movement of the patch in the intervening time period could easily account for this measured difference. Regardless, this region is one of very high biomass and productivity.

GTP levels ranged from a low of non-detectable to a high of 905.8 pM, with an average value of 102.3 pM. Figure 13 shows the relative amounts of protein synthesis which occurred. The highest values of GTP were co-located with the highest peak in biomass (indicated both by ATP and chlorophyll a), the highest nutrient peaks (both nitrate and phosphate), in the strong temperature gradient in the warmer stratified water at the equatorward edge of the feature. This indicates that the most protein synthesis, or gross productivity, occurred in this region.

After these values were normalized by the amount of biomass present levels of productivity as measured by the ratio, GTP/ATP, were computed. Karl [Ref. 113] has indicated that the highest GTP/ATP ratios, .69, are observed in bacteria which are in a logarithmic growth stage. Additional field data which supports these findings have been acquired both in the highly productive Galapagos hydrothermal vents [Ref. 114] where a high of .89 was measured, and in the anoxic region of the Black Sea [Ref. 115] where bacteria flourish. Unicellular algae, fungi, and zooplankton have much lower ratios due to their relatively slower rates of protein synthesis and growth.

One study which looked at the GTP/ATP ratios in 20 species of unicellular algae in an exponential stage of growth found their ratios to range from .10 to .36 with a mean of .20 /‾Ref. 116_7. Therefore, a community maximum value of .29, as observed in October 1980, would represent an area of relatively high growth rate. When the sampling depth of 2.5m is considered, the average value, .10, is within the range of other surface waters indicated in Table VIII. If significant biomass was excluded from the extraction samples which was one possibility indicated by the discrepancy between ATP and chlorophyll a levels, the productivity values would be altered. Since larger organisms have lower ratios, the indicated productivity would correspondingly be lowered.

Figures 14, 18 and 19 illustrate that the specific productivity, measured by GTP/ATP levels, is also high within these areas. This indicates, as do the correlation statistics themselves, that the productivity both absolute, GTP, and specific, GTP/ATP, are most highly correlated with the biomass indicators, ATP and chlorophyll, and nutrients, nitrate and phosphate, in the "New Water," indicating a healthy rapidly growing microbial population. These productivity indicators are also most highly negatively correlated with temperature in the "New Water" indicating that higher productivity is occurring in regions of relatively low temperatures. Additionally, the

correlation of GTP/ATP to GTP indicates that the high specific productivity is occurring where there is high absolute productivity in the "New Water." Conversely, there may be high rates of specific productivity occurring in the "Old Water" but as the correlation statistics indicate these may not be areas of high absolute productivity. In the "Old Water" areas there are indications, Figures 14 and 20, that the smaller populations are still actively growing despite the low levels of nitrate in these areas. Although the biomass is subject to nitrate limitation in the "Old Water" mass, it is apparent from the levels of synthesis still underway that the biological community has not yet sensed and responded to this environmental condition. Exponentially growing algal cells which are transferred to a medium which is nitrate limited, or becomes so, can retain their capacity for photosynthesis and growth for several hours /¯Ref. 117, 118, 119_7. Another study indicated that the effects of varying nutrient concentrations would not effect photosynthesis for at least 24 hours /¯Ref. 120_7. Since growth rate does not depend on current environmental nutrient conditions but upon the nutrient levels during a period of time preceding the time at which the growth rate determination is made, the assumption of steady state conditions may not be valid. A possibility exists that consumption occurred with a subsequent time lag in the growth response. Caperon and Meyer /¯Ref. 121_7 have

postulated that "the relationship between growth rate and limiting nutrient is provided only by the variable internal nutritional state." One study observed a diurnal pattern for internal nitrate levels their results implying that the assimilation and reduction of nitrate are not in phase /‾Ref. 122_7. It was pointed out that these temporal variations in metabolism make it difficult to relate environmental nutrient levels to growth. Lower chlorophyll a values in the "Old Water" in conjunction with the high productivity values may indicate that the phytoplankton are responding to the nitrogen limitation in the environment by mobilizing reservoirs of amino-nitrogen which are bound to the chlorophyll in the photosynthetic unit of the organism /‾Ref. 123_7. Based on studies of a typical algal species, Monodus subterraneus, cell composition has been shown to vary significantly between cells in an exponential stage of growth and cultures which were subjected to nitrogen deficiencies /‾Ref. 124_7. When in a logarithmic stage of growth, protein accounted for approximately 70 percent of the dry weight of the organism, with relatively high percentages of chlorophyll and nucleic acids. Inversely, cells which had been subjected to nitrogen limitation had a composition of less than ten percent protein, with relatively low percentages of chlorophyll and nucleic acids. The photosynthetic efficiency per chlorophyll a (i.e., growth rate) varies inversely with the size of the photosynthetic unit,

indicating that even though a small amount of chlorophyll may be present it may be indicative of higher productivity [Ref. 125].

Another explanation for the high growth rates which occur in these regions of low nitrate concentration could be that ammonium is serving as the source of inorganic nitrogen in these areas, maintaining the indicated growth rates. Ammonium is more easily assimilated than nitrate [Ref. 126, 127]. It is generally assumed that nitrate is the principal source of inorganic nitrogen in regions of upwelling, but in the nitrate poor regions observed in the "Old Water" it is possible that ammonium plays a more significant role. Investigators have shown that ammonium provides approximately 35 percent of the inorganic nitrogen assimilated by phytoplankton in southern California coastal waters, only ten percent of which is attributable to human input [Ref. 128].

Another explanation for the high growth rates observed in these areas could be attributed to varying species composition. Some species are able to maintain a high growth rate at very low levels of nitrate, .05 μM [Ref. 129]. Without knowing the species composition or ammonium levels in these regions it is difficult to interpret which explanation is most probable for maintaining high growth rates in areas of apparent nitrogen limitation.

A survey of other investigations indicates that some researchers have similarly found higher growth rates associated with nutrient poor waters [Ref. 130]. Since "at steady state it is possible to have simultaneously low or undetectable residual nutrient levels and high growth rates regardless of the biomass concentration" [Ref. 131], it is apparent that the available nutrient supply limits the total biomass rather than the actual growth rate. This supports the continuous culture hypothesis which maintains that "the growth rate of the organisms is ...equal to the dilution rate," remaining "completely independent of the concentration of limiting nutrient in the medium feed" [Ref. 132]. In all categories, nitrate was more significantly correlated to productivity than was phosphate indicating that the nitrate level is the limiting nutrient whose "dilution rate" is responsible for growth or the lack thereof within this region. In the "New Water" there is a positive correlation between both of the nutrients and growth whereas the correlation is negative in the "Old Water," indicating that the nutrient concentration in the "New Water" has a positive influence on productivity.

Productivity as measured by ΔATP/ATP indicated a much higher level of productivity. This measurement is based on the supposition that ΔATP is an accurate reflection of the amount of GTP present [Ref. 133]. Since the indicated maximum is greater than that observed in bacteria

in a logarithmic growth phase (with the constant effect of UTP removed), these values are unrealistic. An experiment performed by Bronsink [Ref. 134] showed a high correlation between ΔATP and GTP when known concentrations of binucleotide solutions containing only GTP and ATP were measured. It has been assumed that the other nucleotide triphosphates, namely UTP and CTP, form a constant percentage of the Δ ATP value and can thus be eliminated from consideration when levels of GTP are determined in this way. UTP represented 47 percent of the ΔATP value in one study [Ref. 135]. When this percentage is removed from the calculated Δ ATP values, the Δ ATP/ATP ratios for the cruise data become: .85, high; .05, low; .28, mean. When values of productivity were enzymatically determined, GTP/ATP were correlated to the productivity measurements obtained through calculations of Δ ATP/ATP and a correlation of -.04 was obtained. These results indicate that GTP should be enzymatically determined from field data. Results of an experiment [Ref. 136], which determined the levels of the four nucleotides in Neurospora crassa during exponential growth in different mediums, support this conclusion.

B. CARBON-14 UPTAKE EXPERIMENT

Table V contains the results from the ^{14}C uptake-productivity experiment. Regardless of the way in which the data are manipulated, the assimilation number,

representing the amount of phytoplankton production determined by ^{14}C uptake normalized to the amount of phytoplankton biomass present, is highly correlated to the productivity ratio GTP/ATP. The absolute productivity represented by raw ^{14}C uptake values was similarly well correlated with the GTP values.

The results of this experiment lend credence to the hypothesis that the productivity ratio represented by GTP/ATP is a reasonable indicator of specific production and GTP levels are a good measure of the absolute productivity. Since phytoplankton represent approximately 90 percent of the microbial biomass present in the microplankton /‾Ref.137_7, and since ^{14}C uptake measures primary productivity both GTP and GTP/ATP could prove to be useful measurements for mapping relative rates of absolute and specific productivity, respectively, in the open ocean.

C. TIGRIOPUS CALIFORNICUS PRODUCTIVITY EXPERIMENT

Baugh /‾Ref. 138_7 obtained data on five groups of *Tigriopus californicus*, each group selected to represent a different stage in population growth. The "all-gravid" female group had the highest RNA/DNA ratio of 4.62, followed with ratios of 3.84 for the "young" group, 3.15 for the "mixed" group, 2.16 for the "all-but-gravid" group, and 1.08 for the "old" group.

Determination of GTP/ATP ratios in this species showed a similar relationship between the gravid and all-but-gravid

groups (Fig. 7). The GTP/ATP ratios in the gravid and all-but-gravid groups were determined to be .125 and .099, respectively. This relationship indicates that a higher rate of protein synthesis occurred in the gravid females, which is in accordance with Baugh's results. In contrast, the highest GTP/ATP ratio was observed in the mixed population group containing individuals between 400-500 μm in size. The average ratio of this size fraction was .189, indicating that a higher rate of protein synthesis occurred in this group than in either of the other population subgroups analyzed. Even if the mixed population samples which were subsampled, extracted, analyzed, and averaged were different from the mixed population group selected by Baugh, his results indicate that all other groups selected for study had lower levels of RNA to DNA, and, hence, protein synthesis, than the gravid group. Because of this inconsistancy, results of this experiment indicate that the GTP/ATP ratio may not be as reliable a measure of growth in marine zooplankton as it is in phytoplankton or the RNA/DNA ratio may not be a reliable measure of growth rate.

V. CONCLUSIONS

The nucleotide ratio, GTP/ATP, was shown to be a good indicator of specific community production (principally phytoplankton). There appears to be a good agreement with protein biosynthesis because of the correlation of this ratio with ^{14}C assimilation numbers and the correlation of GTP concentrations with raw ^{14}C uptake values. Use of this ratio to map specific community biosynthesis within oceanic features, both spatially and temporally, could prove invaluable in understanding the nonconservative processes which occur in the oceanic environment. The simultaneous determination of ΔATP and GTP provided evidence that ΔATP is not always a reliable estimator of the amount of GTP in naturally occurring community microbial populations. In view of this finding, enzymatic determination of GTP is necessary for productivity analyses. It may be possible to extend knowledge of the direct relationship between primary productivity and nutrient levels to the more subtle relationship between primary productivity and changes in physical forcing functions.

Some interesting conclusions can be drawn from the interpretation of the October 1980 cruise. The highest GTP levels or absolute production was found where the highest ATP or chlorophyll biomass was associated with strong temperature and nutrient gradients. The stratified

waters bordering the equatorward edge of the cold nutrient rich upwelled water provided the conditions which were favorable for this development. Quantitative determination of the "dilution rate" (nutrient flux) and its relationship to the growth rate (GTP/ATP) will determine the influence of the changing nutrient field and its subsequent impact on the biological field [Ref. 139]. A better understanding of the surface circulation of upwelling features is necessary before this determination will be possible. Once the impact of the nutrient flux can be determined quantitatively, models and predictive equations can be developed based on the "natural chemostat" analogy [Ref. 140, 141, 142], where the rate of nutrient flux can be directly related to the growth rate of the phytoplankton. It may then be possible, given satellite information which has been corrected for prevailing atmospheric conditions, to deduce nutrient maps from satellite derived sea surface temperatures and to extrapolate these findings to infer the distribution of biomass and productivity. Studies of features in all stages of development will be necessary before a model can be developed to predict potential biomass location and growth potential. This prediction would necessarily be a function of the depth of the source water which determines the nutrient concentrations and, thus, the absolute biological potential of any individual system. The depth of the source water is dependent on the age of

the feature, season, and recent wind stress /‾Ref. 143_7. Further study of the spatial and temporal extent of steady state conditions and measurements of flux both through the sea surface and the thermocline would be desirable for expansion of these results into open ocean regions.

Since an increase in biological activity can alter the optical properties of seawater and increase ambient noise levels and reverberation, significantly degrading Antisubmarine Warfare (ASW) operations, it is important to gain a better understanding of the distribution and development of biomass. Such understanding could be incorporated into optical and acoustical prediction models for direct military application.

APPENDIX A

R/V ACANIA CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			0.6						
			1.2	0.00	0.83				14.80
			1.9	0.00	0.83	3.8	225.6		14.80
			2.5	0.00	0.80				15.10
			3.1	0.00	0.83				15.00
			3.7	8.10	1.04				15.00
			4.3	7.47	1.93				15.20
			4.9						
1700	36 1.2	121 44.1	4.9	7.15	1.03		165.0	2.59	15.30
			5.4	7.28	1.01			2.54	15.20
			5.9	7.34	1.02			2.50	15.00
			6.4	6.77	0.99			2.57	15.20
			7.0	6.19	0.95			2.62	15.30
			7.5	6.19	0.98		157.2	2.54	15.20
			8.0	6.26	0.95			2.52	15.30
			8.6	6.13	0.94			2.64	15.40
			9.1	5.33	0.91			2.75	15.30
			9.6	5.75	0.93			2.60	15.20
			10.2	5.68	0.91	6.6	404.8	2.58	15.50
			10.7	5.68	0.91			2.60	15.50
			11.2	5.62	0.91			2.59	15.40
			11.8	5.68	0.91			2.59	15.50
			12.3	5.68	0.91			2.39	15.50
			12.8						
1730	36 4.6	121 47.2	12.8	5.75	0.94		133.2	2.49	15.40
			13.4	5.68	0.93			2.44	15.60
			13.9	5.56	0.91			2.38	15.60
			14.5	5.24	0.89			2.35	15.70
			15.0	5.17	0.89			2.29	15.50
			15.5	5.05	0.89	10.1	143.8	2.26	15.60
			16.1	4.78	0.89			2.23	15.60
			16.6	4.93	0.89			2.30	15.50
			17.2	4.78	0.89			2.24	15.40
			17.7	4.78	0.90			2.25	15.50
			18.3	4.98	0.89	16.6	197.2	2.24	15.30
			18.8	4.78	0.90			2.17	15.50
			19.3	5.05	0.92			2.19	15.40
			19.9	5.05	0.91			2.29	15.30
			20.4	5.17	0.91			2.69	15.30
			21.0						
1800	36 8.2	121 50.3	21.0	5.17	0.91	33.3	191.1	2.95	15.50
			21.5	5.24	0.93			3.16	15.60
			22.1	5.24	0.94			3.65	15.50
			22.7	5.24	0.93			3.99	15.40
			23.2	5.24	0.93			4.29	15.30
			23.8	5.24	0.94		228.7	4.59	15.30
			24.3	5.24	0.97			4.78	15.50
			24.9	5.30	0.97			5.34	15.50
			25.4	5.43	0.96			5.97	15.20
			26.0	5.37	0.96			5.83	15.00
			26.5	5.49	0.95	9.1	282.2	6.50	15.00
			27.1	5.62	0.97			7.84	14.90
			27.7	5.49	0.98			9.09	14.90

CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			28.2	5.52	0.97			10.58	14.00
			28.6	6.19	1.02			12.62	13.80
			29.3						
1830	36 12.2	121 53.1	29.3	6.77	1.03	231.4	838.1	13.93	13.70
			29.9	6.58	1.03			14.38	13.70
			30.5	6.93	1.03			14.41	13.80
			31.1	8.10	1.10			14.36	14.10
			31.7	9.51	1.20			14.31	14.60
			32.2	9.44	1.14			13.66	14.50
			32.8	9.25	1.12			13.82	14.50
			33.4	8.74	1.08			13.84	14.30
			34.0	7.85	1.04			13.78	14.30
			34.6	6.96	0.99			13.94	14.30
			35.2	6.32	0.95			13.80	14.40
			35.7	6.34	0.91			13.74	14.30
			36.3	5.68	0.90			13.90	14.20
			36.9	6.13	0.92			13.99	14.20
			37.5	6.70	0.94			14.16	14.20
			38.0						
1900	36 16.2	121 56.1	38.0	7.09	0.97	143.0	901.0	14.25	14.10
			38.6	7.21	0.97			14.97	14.00
			39.1	7.28	0.98			16.27	13.90
			39.6	7.34	0.99			16.12	13.90
			40.2	7.34	1.01			15.41	14.00
			40.7	7.40	1.00	133.9	875.2	14.93	14.00
			41.3	7.15	1.02			14.78	14.10
			41.8	6.64	1.03			14.20	14.10
			42.4	6.58	1.03			14.95	14.10
			42.9	6.33	1.06			15.04	13.70
			43.4	7.09	1.08	48.7	464.9	15.13	14.20
			44.0	7.21	1.10			14.96	13.90
			44.5	7.47	1.10			14.71	13.90
			45.1	7.59	1.10			13.68	13.80
			45.6	7.72	1.08			14.88	13.00
			46.3						
1930	36 20.6	121 58.7	46.3	7.59	1.06	170.4	830.4	17.20	13.00
			46.9	7.40	1.03			20.28	13.30
			47.6	7.02	1.02			25.43	12.80
			48.2	6.96	1.02			23.08	12.60
			48.9	7.38	1.08			23.05	12.60
			49.5	10.14	1.21	287.9	1325.2	22.51	12.60
			50.2	11.35	1.29			19.91	12.00
			50.8	10.41	1.28			18.86	13.40
			51.2						
1940	36 22.1	122 1.0	51.2	9.76	1.23			14.55	14.10
			51.6	9.38	1.21			14.11	14.20
			52.1	9.70	1.23		645.7	13.41	14.20
			52.5	9.57	1.24			12.84	13.70
			52.9	9.38	1.20			11.92	13.80
			53.3	9.44	1.24			11.58	13.90
			53.7	9.63	1.25			11.49	13.50
			54.2	9.70	1.25	69.1	755.9	12.55	13.50
			54.6	9.38	1.26			13.83	13.20
			55.0					13.96	13.10

R/V ACANIA CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			55.4					13.48	13.10
			55.8					11.80	13.20
			56.3			113.0	1305.2	10.95	13.30
			56.7					6.81	13.60
			57.1					5.58	13.40
			57.5					5.36	13.50
			57.9					5.11	13.70
			58.5						
2030	36 17.5	122 3.3	58.5					5.12	14.20
			59.1			32.3	454.6	4.48	14.70
			59.6					4.16	15.60
			60.2					3.59	15.80
			60.7					3.18	15.80
			61.3					3.24	15.60
			61.8					3.26	15.50
			62.4					3.25	15.50
			62.9					3.17	15.60
			63.5					3.01	15.70
			64.1				139.4	2.91	15.80
			64.6					2.96	15.90
			65.2					2.90	15.90
			65.7			17.3	281.4	2.75	16.00
			66.3					2.60	16.00
			66.8						
2100	36 13.3	122 5.1	66.8					2.68	16.10
			67.4					2.68	16.10
			67.9					2.71	16.10
			68.5					2.66	16.10
			69.1					2.79	16.10
			69.6			66.4	263.6	2.81	16.10
			70.2					2.86	16.20
			70.7					2.83	16.20
			71.3					2.82	16.30
			71.8					2.90	16.40
			72.4			26.2	181.8	2.94	16.40
			72.9					3.11	16.30
			73.5					3.16	16.40
			74.1					3.30	16.40
			74.6			31.2	402.2	3.42	16.40
			75.2						
2130	36 9.1	122 7.1	75.2					3.38	16.00
			75.8					3.22	16.00
			76.4					3.21	16.20
			77.0					3.20	16.10
			77.6					2.99	16.10
			78.2			52.7	337.2	3.03	16.10
			78.8					3.05	16.10
			79.4					2.95	16.20
			80.1					2.88	16.50
			80.7					2.87	16.70
			81.3			50.8	421.5	2.86	16.60
			81.9	0.00	0.92			2.85	16.50
			82.5	0.00	0.88			2.84	15.90

R/V ACANIA CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			83.1	0.00	0.86			2.80	15.80
			83.7	0.00	0.85	17.3	318.5	2.77	15.90
			84.3						
2200	36 4.7	122 9.4	84.3	0.00	0.83			2.92	15.90
			84.8	0.00	0.81			2.86	16.10
			85.4	0.00	0.81			2.85	15.90
			86.0	0.00	0.79			2.64	16.80
			86.6	0.00	0.81			2.41	16.90
			87.2	0.00	0.81			2.63	16.70
			87.7	0.00	0.81	75.5	545.7	2.94	16.50
			88.3	0.00	0.81			2.90	16.60
			88.9	0.00	0.81			2.73	16.70
			89.5	0.00	0.83			2.69	16.40
			90.1	0.00	0.81	114.2	230.7	2.68	16.60
			90.6	0.00	0.81			2.67	16.30
			91.2	0.00	0.79			2.66	16.70
			91.8	0.00	0.78			2.70	16.70
			92.4	0.00	0.78			2.82	16.70
			93.0						
2230	36 0.1 .	122 11.2	93.0	0.00	0.76	161.5	1294.2	2.84	16.50
			93.6	0.00	0.76			2.80	16.40
			94.2	0.00	0.76			2.74	16.40
			94.8	0.00	0.76			2.62	16.40
			95.4	0.00	0.76			2.59	16.50
			95.9	0.00	0.76			2.57	16.50
			96.5	0.00	0.76			2.56	16.80
			97.1	0.00	0.76			2.55	17.10
			97.7	0.00	0.76			2.98	16.80
			98.3	0.00	0.78			3.04	16.00
			98.9	0.00	0.78			3.21	16.40
			99.5	0.00	0.76			2.97	16.50
			100.1	0.00	0.76			2.98	16.70
			100.7	0.00	0.76			2.69	16.90
			101.3	0.00	0.76			2.61	17.00
			101.8						
2300	35 55.6	122 12.9	101.8	0.00	0.78			2.47	17.00
			102.4	0.00	0.78			2.51	17.00
			103.0	0.00	0.78			2.55	17.00
			103.6	0.00	0.78			2.56	16.90
			104.1	0.00	0.78	63.8	158.4	2.57	16.60
			104.7	0.00	0.78			2.72	16.60
			105.3	0.00	0.76			2.80	16.60
			105.8	0.00	0.76			2.81	16.70
			106.4	0.00	0.76			2.84	16.70
			107.0	0.00	0.78			2.88	16.60
			107.5	0.00	0.78	88.9	194.2	2.93	16.50
			108.1	0.00	0.78			2.73	16.50
			108.7	0.00	0.78			2.74	16.50
			109.2	0.00	0.78			2.38	16.50
			109.8	0.00	0.78			2.37	16.70
			110.4	0.00	0.78	91.4	221.9	2.28	17.40
			110.9	0.00	0.79			2.04	16.20
			111.3						
2334	35 50.7	122 15.4	111.3	0.00	0.79			2.08	16.00

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			111.7	0.00	0.78			2.09	16.60
			112.1	0.00	0.76			2.06	16.50
			112.5	0.00	0.76	92.6	179.3	2.02	16.40
			112.9	0.00	0.78			2.32	16.40
			113.2	0.00	0.78			2.42	16.50
			113.6	0.00	0.78			2.45	16.50
			114.0	0.00	0.78			2.24	16.50
			114.4	0.00	0.78			2.38	18.20
			114.8	0.00	0.78			2.22	17.40
			115.1	0.00	0.78			2.31	17.00
			115.5	0.00	0.78			2.34	16.90
			115.9	0.00	0.78			2.24	16.90
			116.5						
2400	35 52.9	122 17.4	116.5	0.00	0.78	181.0	910.8	2.14	16.60
			117.0	0.00	0.78			2.29	16.40
			117.5	0.00	0.78			2.36	16.10
			118.1	0.00	0.78			2.32	16.70
			118.6	0.00	0.78			2.49	16.70
			119.2	0.00	0.78			2.46	16.50
			119.7	0.00	0.78			2.42	16.40
			120.3	0.00	0.78			2.47	16.30
			120.8	0.00	0.78			2.49	16.20
			121.3	0.00	0.78			2.50	16.20
			121.9	0.00	0.78			2.52	16.10
			122.4					2.50	16.10
			123.0					2.49	16.40
			123.5					2.47	16.50
			124.1					2.46	16.40
			124.6					2.42	16.30
			125.1					2.41	16.20
			125.7						
0034	35 57.3	122 20.6	125.7					2.34	16.20
			126.3					2.40	16.20
			126.8					2.42	15.90
			127.4					2.46	16.10
			128.0					2.57	16.00
			128.6					2.55	16.00
			129.1	0.00	0.85			2.53	15.90
			129.7	0.00	0.86			2.52	16.50
			130.3	0.00	0.85			2.52	16.10
			130.8	0.00	0.85			2.48	16.10
			131.4	0.00	0.86			2.47	16.10
			132.0	0.00	0.83			2.55	16.10
			132.5	0.00	0.85			2.52	16.20
			133.1						
0100	36 0.4	122 23.1	133.1	0.00	0.83			2.43	16.00
			133.7	0.00	0.85			2.45	16.20
			134.3	0.00	0.85			2.40	16.40
			134.8	0.00	0.85			2.36	16.30
			135.4	0.00	0.85			2.35	16.40
			136.0	0.00	0.83			2.33	16.30
			136.6	0.00	0.85			2.31	16.20
			137.2	0.00	0.83			2.31	16.10

R/V ACANIA

CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			137.7	0.00	0.85			2.34	16.20
			138.3	0.00	0.83			2.42	16.40
			138.9	0.00	0.85			2.37	16.40
			139.5	0.00	0.83			2.32	16.10
			140.1	0.00	0.85			2.32	16.00
			140.7	0.00	0.85			2.33	16.00
			141.2	0.00	0.85			2.33	16.10
			141.8						
0130	36 4.7	122 26.4	141.8	0.00	0.85			2.42	16.20
			142.3	0.00	0.85			2.43	16.00
			142.8	0.00	0.85			2.43	16.10
			143.3	0.00	0.85			2.39	16.10
			143.8	0.00	0.85			2.39	16.10
			144.3	0.00	0.85			2.37	16.00
			144.9	0.00	0.85			2.32	16.10
			145.4	0.00	0.86			2.30	16.30
			145.9	0.00	0.86			2.27	16.20
			146.4	0.00	0.86			2.22	16.30
			146.9	0.00	0.86			2.17	16.20
			147.5	0.00	0.85			2.15	16.30
			148.0	0.00	0.85			2.16	16.40
			148.5	0.00	0.86			2.17	16.30
			149.0	0.00	0.86			2.16	16.30
			149.4						
0200	36 7.9	122 29.5	149.4	0.00	0.85	30.0	172.2	2.21	16.30
			149.8	0.00	0.88	33.0	96.7	2.60	15.70
			150.2	0.00	0.88			2.89	15.70
			150.6	0.00	0.90			3.13	15.90
			151.0	0.00	0.90			3.34	15.60
			151.4	0.00	0.88			3.25	16.00
			151.8	0.00	0.88	42.4	141.4	3.42	16.30
			152.2	0.00	0.88			3.82	16.50
			152.6	0.00	0.90			4.02	16.50
			153.0	0.00	0.90			4.19	16.40
			153.4	0.00	0.90			4.37	16.30
			153.9						
0230	36 9.4	122 26.4	153.9	0.00	0.90	139.9	426.9	4.56	16.20
			154.4	0.00	0.88			4.76	16.10
			155.0	0.00	0.88			4.95	16.10
			155.5	0.00	0.88			5.18	16.00
			156.1	0.00	0.88			5.12	16.00
			156.6			84.6	299.2	5.20	15.90
			157.2					5.37	15.90
			157.7					5.70	15.60
			158.2					5.64	14.80
			158.8					5.41	14.40
			159.3			70.5	293.5	5.61	14.10
			159.9					5.95	14.00
			160.4					7.72	13.90
			161.0	0.00	0.94			8.82	13.90
			161.5	0.00	0.97			9.16	14.00
			162.1						
0300	36 11.5	122 21.6	162.1	0.46	0.97	173.7	617.4	10.25	14.10
			162.7	0.46	0.99			9.39	14.60

R/V ACANIA CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			163.3	0.12	0.95			7.41	14.80
			163.9	0.00	0.88			5.73	14.90
			164.4	0.00	0.85			6.04	14.80
			165.0	0.00	0.85			5.66	14.70
			165.6	0.00	0.86			5.64	14.60
			166.2	0.00	0.86			6.07	14.60
			166.8	0.00	0.83			6.24	14.70
			167.4	0.00	0.83			5.68	14.70
			168.0	0.00	0.81	61.0	1035.0	5.39	14.70
			168.5	0.00	0.81			4.72	14.70
			169.1	0.00	0.81			4.61	14.60
			169.7	0.00	0.81			4.87	14.50
			170.3	0.00	0.81			4.57	14.50
			170.9	0.00	0.83	253.1	1478.7	4.64	14.50
			171.5	0.00	0.83			4.02	14.60
			172.1	0.00	0.83			3.40	14.70
			172.6	0.00	0.83			3.11	15.00
			173.2	0.00	0.81			2.86	15.70
			173.8						
0340	36 14.7	122 15.0	173.8	0.00	0.85	13.1	154.4	2.72	15.70
			174.5	0.00	0.85			2.82	15.50
			175.1	0.00	0.85			2.87	15.60
			175.7	0.00	0.86			3.12	15.60
			176.3	0.00	0.85			3.50	15.40
			176.9	0.00	0.85	23.0	184.2	3.43	15.60
			177.5	0.00	0.85			3.47	15.60
			178.1	0.00	0.83			3.65	15.40
			178.7	0.00	0.83			3.63	15.40
			179.3	0.00	0.83			3.52	15.30
			179.9						
0400	36 16.5	122 11.7	179.9	0.00	0.85	54.6	260.6	3.67	15.20
			180.4	0.00	0.85			4.32	15.10
			180.9	0.00	0.85			4.63	15.00
			181.4	0.00	0.85			5.71	14.80
			181.9	0.00	0.85			6.22	14.50
			182.5	0.00	0.85	117.7	416.9	6.60	14.50
			183.0	0.00	0.86			6.50	14.50
			183.5	0.00	0.85			7.00	14.40
			184.0	0.00	0.86			7.70	14.10
			184.5	0.00	0.86			7.61	13.80
			185.0	0.00	0.88	235.8	731.9	7.23	13.70
			185.6	0.00	0.90			7.91	13.70
			186.1	0.00	0.90			9.23	13.70
			186.6	0.00	0.92			10.31	13.50
			187.1	0.00	0.94			13.71	13.40
			187.7						
0430	36 21.0	122 7.3	187.7	0.12	0.95	175.6	654.9	18.00	13.20
			188.2	0.12	0.95			20.21	13.10
			188.7	0.30	0.99			20.89	13.10
			189.2	0.80	0.97			19.53	13.50
			189.8	1.13	1.06			19.70	13.70
			190.3	1.30	1.02	143.4	876.2	20.51	13.50
			190.8	1.47	1.01			21.75	13.50

R/V ACANIA

CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			191.4	1.47	0.99			23.39	13.30
			191.9	0.30	0.97			22.86	13.30
			192.4	0.46	0.95			22.73	13.40
			193.0	0.46	0.95	139.9	601.0	24.13	13.40
			193.5	0.46	0.95			25.46	13.40
			194.0	0.30	0.95			24.63	13.50
			194.6	0.30	0.97			24.03	13.50
			195.1	0.30	0.95			26.02	13.60
			195.6						
0500	36 21.0	122 2.8	195.6	0.46	0.95	215.9	501.3	28.20	13.60
			196.1	0.46	0.95			29.87	13.40
			196.6	0.46	0.95			32.90	13.20
			197.1	0.12	0.95			35.31	13.60
			197.6	0.12	0.94			40.56	13.00
			198.1	0.46	0.95	335.0	784.1	43.83	12.90
			198.6	0.46	0.97			47.16	12.70
			199.1	0.30	0.99			55.29	12.70
			199.6	1.13	1.01	905.8	3391.8	56.40	12.70
			200.1	1.13	1.01			42.06	13.00
			200.6	1.47	1.01	142.7	432.1	35.03	13.00
			201.1	1.47	1.02			31.36	13.20
			201.6	1.47	1.02			26.13	13.40
			202.1	1.13	1.02			25.91	13.40
			202.6	1.47	1.04			26.93	13.50
			203.1	1.80	1.06			26.95	13.50
			203.6	1.13	1.02			27.68	13.50
			204.1	0.80	1.01			27.69	13.60
			204.6	0.46	0.97			29.28	13.70
			205.1	0.12	0.95			27.81	13.60
			205.6						
0540	36 25.8	122 1.0	205.6	0.00	0.94			26.40	13.70
			206.1	0.00	0.94			25.02	13.70
			206.6	0.00	0.94			24.91	13.70
			207.2	0.00	0.92			24.47	13.70
			207.7	0.00	0.92			24.47	13.70
			208.2	0.00	0.92			24.25	13.60
			208.7	0.00	0.92			24.14	13.50
			209.2	0.00	0.92			24.03	13.40
			209.8	0.00	0.95			23.81	13.40
			210.3	0.00	0.94			23.69	13.40
			210.8						
0600	36 28.7	122 1.1	210.8	0.00	0.95			23.47	13.30
			211.3	0.12	0.95			23.14	13.20
			211.8	0.12	0.95			23.54	13.10
			212.3	0.12	0.97			23.52	13.10
			212.9	0.46	0.99			23.90	13.00
			213.4	0.46	0.99			23.86	13.00
			213.9	0.46	0.99			23.83	13.00
			214.4	0.46	0.99			23.78	12.90
			214.9	0.80	1.01			22.95	12.90
			215.5	1.13	1.04			22.71	12.70
			216.0	1.47	1.02			22.86	12.70
			216.5	1.47	1.02			22.91	12.70

R/V ACANIA CHEMICAL MESOSCALE (CRUISE XIII)

TIME GMT	LATITUDE NORTH	LONGITUDE WEST	DISTANCE KM	NO3 UM	PO4 UM	GTP PICOMOLAR	ATP NG/L	CHL A MG/M3	TEMP DEG C
			217.0	1.13	1.06			23.93	12.60
			217.5	1.47	1.06			23.53	12.50
			218.1	2.14	1.08			23.65	12.40
			218.6	2.14	1.08			23.48	12.20
			219.1	2.14	1.10			23.40	12.10
			219.6	2.48	1.11				12.00
			220.1	2.48	1.11				11.90
			220.6	3.15	1.15				11.80
			221.2	3.92	1.17				11.80
			221.7	3.82	1.18				12.00
			222.2	4.49	1.22				12.00

LIST OF REFERENCES

1. Stavn, R.H., "The Horizontal-Vertical Distribution Hypothesis: Langmuir Circulation and *Daphnia* Distributions," *Limnology and Oceanography*, Vol. 16, p. 453-466, 1971.

2. Huntsman, S.A. and Barber, R.T., "Primary Production off Northwest Africa: the Relationship to Wind and Nutrient Conditions," *Deep-Sea Research*, Vol. 24, p. 25-33, 1977.

3. Lekan, J.F. and Wilson, R.E., "Spatial Variability of Phytoplankton Biomass in the Surface Waters of Long Island," *Estuarine and Coastal Marine Science*, Vol. 6, p. 239-251, 1978.

4. Therriault, J.C. and Platt, T., "Spatial Heterogeneity of Phytoplankton Biomass and Related Factors in the Near-Surface Waters of an Exposed Coastal Embayment" *Limnology and Oceanography*, Vol. 23, No. 5, p. 888-899, 1978.

5. Denman, K.L., "Convariability of Chlorophyll and Temperature in the Sea," *Deep-Sea Research*, Vol. 23, p. 539-550, 1976.

6. Turpin, D.H. and Harrison, P.J., "Limiting Nutrient Patchiness and its Role in Phytoplankton Ecology," *Journal of Experimental Marine Biological Ecology*, Vol. 39, p. 151-166, 1979.

7. Reid, J.L., Roden, G.I., and Wyllie, J.G., *Studies of the California Current System, Contribution from the Scripps Institution of Oceanography*, Progress report-California Cooperative Oceanic Fisheries Investigation, July 1, 1956-January 1, 1958.

8. Traganza, E.D., Conrad, J.W., and Breaker, L.C., "Satellite Observations of a 'Cyclonic Upwelling System' and 'Giant Plume' in the California Current," In: *Coastal Upwelling*, American Geophysical Union, Washington, D.C., 1981.

9. Bronsink, S.H., *Microplanktonic ATP-Biomass and GTP-Productivity Associated with Upwelling off Point Sur, California*, Master's Thesis, Naval Postgraduate School, Monterey, California, 1980.

10. Traganza, E.D., Conrad, J.W., and Breaker, L.C., "Satellite Observations of a 'Cyclonic Upwelling

System' and 'Giant Plume' in the California Current," In: Coastal Upwelling, American Geophysical Union, Washington, D.C., 1981.

11. Eppley, R.W. and others, "A Study of Plankton Dynamics and Nutrient Cycling in the Central Gyre of the North Pacific Ocean," Limnology and Oceanography, Vol. 18, No. 4, 1973.

12. Goldman, J.C., McCarthy, J.J., and Peavey, D.G., "Growth Rate Influence on the Chemical Composition of Phytoplankton in Oceanic Waters," Nature, Vol. 279, 1979.

13. Tranter, D.J., Parker, R.R., and Cresswell, G.R., "Are Warm-Core Eddies Unproductive?," Nature, Vol. 284, No. 5756, p. 540-542, 1980.

14. Beardall, J. and others, "Phitoplankton Distributions in the Western Irish Sea and Liverpool Bay and their Relation to Hydrological Factors: a progress report," Biologia Contemporanca, Vol. 5, No. 4, p. 163-175, 1978.

15. Savidge, G. and Foster, P., "Phytoplankton Biology of a Thermal Front in the Celtic Sea," Nature, Vol. 271, p. 155-157, 1978.

16. Floodgate, G.D. and others, "Microbiological and Zooplankton Activity at a Front in Liverpool Bay," Nature, Vol. 290, p. 133-136, 1981.

17. Pingree, R.D. and others, "Summer Phytoplankton Blooms and Red Tides Along Tidal Fronts in the Approaches to the English Channel," Nature, Vol. 258, p. 672-677, 1975.

18. Szekielda, K.H., and Suszkowski, D.J., and Tabor, P.S., "Skylab Investigation of the Upwelling off the Northwest Coast of Africa," Journal Cons. Int. Explor. Mer., Vol. 37, No. 3, p. 205-213, 1977.

19. Traganza, E.D. and Austin, D.M., "Nutrient Mapping and the Biological Structure of Upwelling Systems From Infrared and Ocean Color Imagery," Science (in process), 1981.

20. Bronsink, S.H., Microplanktonic ATP-Biomass and GTP-Productivity Associated with Upwelling off Pt. Sur, California, Master's Thesis, Naval Postgraduate School, Monterey, California, 1980.

21. Wroblewski, J.S. and O'Brien J.J., "A Spatial Model of Phytoplankton Patchiness," Marine Biology, Vol. 35, p. 161-175, 1976.

22. Pace, N.R., "Structure and Synthesis of the Ribosomal Ribonucleic Acid of Prokaryotes," Bacteriological Reviews, p. 562-603, December 1973.

23. Karl, D.M., "Occurrence and Ecological Significance of GTP in the Ocean and in Microbial Cells," Applied and Environmental Microbiology, p. 349-355, 1978.

24. Karl, D.M., "Adenosine Triphosphate and Guanosine Triphosphate Determinations in Intertidal Sediments," In Methodology for Biomass Determinations and Microbial Activities in Sediments, ASTM STP 673, C.D. Littlefield and P.L. Seyfried, Eds., American Society for Testing and Materials, p. 5-20, 1979.

25. Lucas-Lenard, J. and Lipmann, F., "Protein Biosynthesis," in E.E. Snell (ed)., Annual Review of Biochemistry, Annual Reviews Inc., Palo Alto, California, Vol. 40, 409-448, 1971.

26. Eccleston, J.F., "Single Turnover Kinetic Studies of Guanosine Triphosphate Hydrolysis and Peptide Formation in the Elongation Factor Tu-dependent Binding of Aminoacyl-tRNA to Escherichia Coli Ribosomes," The Journal of Biological Chemistry, Vol. 255, No. 23, p. 11088-11090, 1980.

27. Chinali, G. and Parmeggiani, A., "The Coupling with Polypeptide Synthesis of the GTPase Activity Dependent on Elongation Factor G," The Journal of Biological Chemistry, Vol. 255, No. 15, p. 7455-7459, 1980.

28. Watson, J.D., Molecular Biology of the Gene, W.A. Benjamin, Inc., p. 331-338, 1977.

29. Volkin, E., and others, "Suppression of the Biosynthesis of Guanosine Triphosphate by Protein Synthesis Inhibitors," The Journal of Biological Chemistry, Vol. 255, No. 19, p. 9105-1909, 1980.

30. Ryther, J.H., "The Measurement of Primary Production," Limnology and Oceanography, Vol. 1, p. 72-84, 1956.

31. Ryther, J.H., and Menzel, D.W., "Comparison of the ^{14}C Technique with Direct Measurement of Photosynthetic Carbon Fixation," Limnology and Oceanography, Vol. 10, p. 490-492, 1965.

32. Eppley, R.W., "An Incubation Method for estimating the Carbon Content of Phytoplankton in Natural Samples," Limnology and Oceanography, Vol. 13, p. 574-582, 1968.

33. Smith, R.J., "Increasing Guanosine 3'-Diphosphate Concentration with Decreasing Growth Rate in Anacystis

nidulans." Journal of General Microbiology, Vol. 113, p. 403-405, 1979.

34. Sokawa, Y., Sokawa, J., and Kaziro, Y., "Regulation of Stable RNA Synthesis and ppGpp Levels in Growing Cells of Escherichia coli," Cell, Vol. 5, p. 69-74, 1975.

35. Franzen, J.S. and Binkley, S.B., "Comparison of the Acid-soluble Nucleotides in Escherichia coli at Different Growth Rates," The Journal of Biological Chemistry, Vol. 236, No. 2, p. 515-519, 1961.

36. Smith, R.C. and Maaloe, O., "Effect of Growth Rate on the Acid-Soluble Nucleotide Composition of Salmonella Typhimurium," Biochimica et Biophysica Acta, Vol. 86, p. 229-234, 1964.

37. Karl, D.M., "Distribution, Abundance, and Metabolic States of Microorganisms in the Water Column and Sediments of the Black Sea," Limnology and Oceanography, Vol. 23, No. 5, p. 936-949, 1978.

38. Karl, D.M., "Occurrence and Ecological Significance of GTP in the Ocean and in Microbial Cells," Applied and Environmental Microbiology, p. 349-355, 1978.

39. Lorenzen, C.J., "A Method for the Continuous Measurement of In Vivo Chlorophyll Concentration," Deep Sea Research, Vol. 13, p. 223-227, 1966.

40. Slovacek, R.E. and Hannan, P.J., "In Vivo Fluorescence Determinations of Phytoplankton Clorophyll a" Limnology and Oceanography, Vol. 22 (5), p. 919-925, 1977.

41. Strickland, J.D. and Parsons, T.R., A Practical Handbook of Seawater Analysis, J.C. Stevenson (ed), Queen's Printer and Comptroller of Stationary, p. 49-62 and 71-76, 1968.

42. Technicon Industrial Systems Industrial Method No. 177-72-WM, Ortho Phosphate in Water and Seawater, January, 1978.

43. Technicon Industrial Systems Technical Publication No. TA 1-0170-20, Operation Manual for the Technicon Auto Analyzer II System, 1972.

44. Technicon Industrial Systems Industrial Method No. 100-70-W/B, Nitrate and Nitrite in Water and Waste Water, January 1978.

45. Technicon Autoanalyzer Industrial Method No. 175-72-WM, *Nitrate and Nitrite in Water and Seawater*, January 1973.

46. Paulson, G.P., *A Study of Nutrient Variations in the Surface and Mixed Layer of Monterey Bay using Automatic Analysis Techniques*, Master's Thesis, Naval Postgraduate School, Monterey, California, 1972.

47. Holm-Hansen, O. and Karl, D.M., "Biomass and Adenylate Energy Charge Determination in Microbial Cell Extracts and Environmental Samples," *Methods in Enzymology*, Vol. 57, p. 73-85, 1978.

48. Ibid

49. DeLuca, M., "Enzyme Reaction and Historical Background," In G.A. Borun (ed.), *ATP Methodology Seminar*, SAI Technology Co., San Diego, California, p. 1-21, 1975.

50. Ibid, p. 1-3.

51. Ibid, p. 2.

52. Holm-Hansen, O. and Karl, D.M., "Biomass and Adenylate Energy Charge Determination in Microbial Ceall Extracts and Environmental Samples," *Methods in Enzymology*, Vol. 57, p. 73-85, 1978.

53. Karl, D.M., "Determination of GTP, GDP, and GMP in Cell and Tissue Extracts," In M.A. DeLuca (ed.), *Methods in Enzymology*, Volume LVII, Academic Press, New York, p. 85-94, 1978.

54. Karl, D.M., "A Rapid and Sensitive Method for the Measurement of Guanine Ribonucleotides in Bacterial and Environmental Extracts," *Analytical Biochemistry*, Vol. 89, p. 581-595, 1978.

55. Ibid, p. 587-588.

56. Karl, D.M. and Holm-Hansen, O., "Effects of Luciferin Concentration on Quantitative Assay of ATP Using Crude Luciferase Preparations," *Analytical Biochemistry*, Vol. 75, p. 110-112, 1976.

57. Luminescent Review Bulletin 202, *ATP Measurements: Theory and Practice*," p. 11, February 1981.

58. Holm-Hansen, O. and Booth, C.R., "The Measurement of ATP in the Ocean and Its Ecological Significance," *Limnology and Oceanography*, Vol. 11, p. 510-519, 1966.

59. Holm-Hansen, O. and Karl, D.B., "Biomass and Adenylate Energy Charge Determination in Microbial Cell Extracts and Environmental Samples," *Methods in Enzymology*, Vol. 57, p. 73-85, 1978.

60. Karl, D.M. and Holm-Hansen, O., "Effects of Luciferin Concentration on Quantitative Assay of ATP Using Crude Luciferase Preparations," *Analytical Biochemistry*, Vol. 75, p. 110-112, 1976.

61. Booth, C., "Instrument Development and Data Processing for the A.T.P. Photometer," in G.A. Borun (ed.), *ATP Methodology Seminar* SAI Technology Co., San Diego, California, p. 104-130, 1975.

62. Karl, D.M., "A Rapid and Sensitive Method for the Measurement of Guanine Ribonucleotides in Bacterial and Environmental Extracts," *Analytical Biochemistry*, Vol. 89, p. 581-595, 1978.

63. Ibid. p. 590.

64. Ibid, p. 590.

65. Booth, C., "Instrument Development and Data Processing for the A.T.P. Photometer," In G.A. Borun (ed.), *ATP Methodology Seminar*, SAI Technology Co., San Diego, California, p. 104-130, 1975.

66. Rowney, J.V., *Gradient Analysis of Phytoplankton Productivity and Chemical Parameters in Polluted and Other Nearshore Habitats*, Master's Thesis, Naval Postgraduate School, Monterey, California, 1973.

67. Jitts, H.R. and Scott, B.D., "The Determination of Zero-Thickness Activity in Geiger Counting of C^{14} Solutions Used in Marine Productivity Studies," *Limnology and Oceanography*, Vol. 6(2), p. 116-123, 1961.

68. Strickland, J.D. and Parsons, T.R., *A Practical Handbook of Seawater Analysis*, J.C. Stevenson (ed), Queen's Printer and Comptroller of Stationary, 1968.

69. Egloff, D.A., *Ecological Aspects of Sex Ratios and Reproduction in Experimental and Field Populations of the Marine Copepod Tigriopus californicus*, Ph.D. Dissertation, Stanford University, California, 1966.

70. Baugh, D.E., *RNA/DNA Ratios in the Estimation of Growth Stages of Oceanic Zooplankton Populations*, Master's Thesis, Naval Postgraduate School, Monterey, California, 1974.

71. Brachet, J., The Biological Role of Ribonucleic Acids, Elsevier, New York, p. 1-49, 1960.

72. Sutcliffe, W.H., Jr., "The Relationship Between Growth Rate and Ribonucleic Acid Concentration in Some Invertebrates," Journal of Fisheries Research Board of Canada, Vol. 27, p. 606-609, 1969.

73. Pease, A.K., The Use of Estimations of Ribonucleic Acid to Predict the Growth Rates of Zooplanktonic Organisms, Master's Thesis, University of British Columbia, 1968.

74. Leick, V., "Ratios Between Content of DNA, RNA, and Protein in Different Micro-Organisms as a Function of Maximal Growth Rate," Nature, Vol. 217, p. 1153-1155, 1968.

75. Baugh, D.E., RNA/DNA Ratios in the Estimation of Growth Stages of Oceanic Zooplankton Populations, Master's Thesis, Naval Postgraduate School, Monterey, California, 1974.

76. Skjoldal, H.R. and U. Bamstedt, "Ecochemical Studies on the Deepwater Pelagic Community of Korsfjorden, Western Norway. Adenine Nucleotides in Zooplankton." Marine Biology, Vol. 42, p. 197-211, 1977.

77. Holm-Hansen, O., "Determination of Microbial Biomass in Ocean Profiles," Limnology and Oceanography Vol. 14, 740-747, 1969.

78. Ibid, p. 744.

79. Holm-Hansen, O., "Carbon/ATP Ratios in Microbial Cultures and in Natural Populations," In G.A. Borun (ed.), ATP Methodology Seminar, SAI Technology Co., San Diego, California, p. 446-473, 1975.

80. Sorokin, Y.I. and Mikheev, V.N., "On Characteristics of the Peruvian Upwelling Ecosystem," Hydrobiologia, Vol. 62, No. 2, p. 165-189, 1979.

81. Holm-Hansen, O., "ATP Levels in Algal Cells as Influenced by Environmental Conditions," Plant Cell Physiology, Vol. 11, p. 689-700, 1970.

82. Karl, D.M., "Occurrence and Ecological Significance of GTP in the Ocean and in Microbial Cells," Applied and Environmental Microbiology, p. 349-355, 1978.

83. Hanson, W.E., Nutrient Study of Mesoscale Thermal Features off Point Sur, California, Master's Thesis, Naval Postgraduate School, Monterey, California, 1980.

84. Traganza, E.D., Conrad, J.W., and Breaker, L.C., "Satellite Observations of a 'Cyclonic Upwelling System' and 'Giant Plume' in the California Current," In: Coastal Upwelling, American Geophysical Union, Washington, D.C., 1981.

85. Traganza, E.D., Nestor, D.A. and McDonald, A.K., "Satellite Observations of a Nutrient Upwelling Off the Coast of California," Journal of Geophysical Research, Vol. 85, No. C7, p. 4101-4106, July 1980.

86. Baugh, D.E., RNA/DNA Ratios in the Estimation of Growth Stages of Oceanic Zooplankton Populations, Master's Thesis, Naval Postgraduate School, Monterey, California, 1974.

87. Wiebe, P.H., "A Computer Model Study of Zooplankton Patchiness and its Effect on Sampling Error," Limnology and Oceanography, Vol. 16, No. 1, p. 29-38, 1971.

88. Therriault, J.C. and Platt, T., "Spatial Heterogeneity of Phytoplankton Biomass and Related Factors in the Near-Surface Waters of an Exposed Coastal Embayment," Limnology and Oceanography, Vol. 23, No. 5, p. 888-899, 1978.

89. Platt, T., Dickie, L.M. and Trites, R.W., "Spatial Heterogeneity of Phytoplankton in a Near-Shore Environment," Journal of Fisheries Research Board of Canada, Vol. 27, p. 1453-1473, 1970.

90. Redfield, A.C., "The Biological Control of Chemical Factors in the Environment," American Science, Vol. 46(3), p. 205-221, 1958.

91. Goldman, J.C., McCarthy, J.J., and Peavey, D.G., "Growth Rate Influence on the Chemical Composition of Phytoplankton in Oceanic Waters," Nature, Vol. 279, 1979.

92. MacIsaac, J.J. and Dugdale, R.C., "The Kinetics of Nitrate and Ammonia Uptake by Natural Populations of Marine Phytoplankton," Deep Sea Research, Vol. 16, p. 45-57, 1969.

93. Qasim, S.Z., Bhattathiri, P.M., and Devassy, V.P., "Growth Kinetics and Nutirent Requirements of Two Tropical Marine Phytoplankters," Marine Biology, Vol. 21, p. 299-304, 1973.

94. Caperon, J., "Population Growth in Micro-Organisms Limited by Food Supply," Ecology, Vol. 48, p. 715-722, 1967.

95. Dugdale, R.C., "Nutrient Limitation in the Sea: Dynamics, Identification, and Significance," Limnology and Oceanography, Vol. 12, p. 685-695, 1967.

96. Thomas, W.H., "Effect of Ammonium and Nitrate Concentration on Chlorophyll Increases in Natural Tropical Pacific Phytoplankton Populations," Limnology and Oceanography, Vol. 15, p. 386-394, 1970.

97. MacIsaac, J.J. and Dugdale, R.C., "Interactions of Light and Inorganic Nitrogen in Controlling Nitrogen Uptake in the Sea," Deep-Sea Research, Vol. 19, p. 209-232, 1972.

98. MacIsaac, J.J. and Dugdale, R.C., "The Kinetics of Nitrate and Ammonia Uptake by Natural Populations of Marine Phytoplankton," Deep Sea Research, Vol. 16, p. 45-57, 1969.

99. Karl, D.M., "Cellular Nucleotide Measurements and Applications in Microbial Ecology," Microbiological Reviews, p. 781, December 1980.

100. Karl, D.M., "Cellular Nucleotide Measurements and Applications in Microbial Ecology," Microbiological Reviews, p. 739-796, December 1980.

101. Bronsink, S.H., Microplanktonic ATP-Biomass and GTP-Productivity Associated with Upwelling off Pt. Sur, California, Master's Thesis, Naval Postgraduate School, Monterey, California, 1980.

102. Steele, J.H. and Baird, I.E., "Relations Between Primary Production, Chlorophyll and Particulate Carbon," Limnology and Oceanography, Vol. 6, 1960.

103. Eppley, R.W., Harrison, W.G., Chisholm, S.W., and Stewart, E., "Particulate Organic Matter in Surface Waters of Southern California and its Relationship to Phytoplankton," Journal of Marine Resources, Vol. 35, p. 671-696, 1977.

104. Perry, M.J., Talbot, M.C., and Alberte, R.S., "Photoadaption in Marine Phytoplankton: Response of the Photosynthetic Unit," Marine Biology (in press 1981).

105. Slovacek, R.E. and Hannan, P.J., "In Vivo Fluorescence Determinations of Phytoplankton Clorophyll a" Limnology and Oceanography, Vol. 22(5), p. 919-925, 1977.

106. Traganza, E.D., Conrad, J.W., and Breaker, L.C., "Satellite Observations of a 'Cyclonic Upwelling System' and 'Giant Plume' in the California Current," In: Coastal Upwelling, American Geophysical Union, Washington, D.C., 1981.

107. Goldman, J.C., McCarthy, J.J., and Peavey, D.G., "Growth Rate Influence on the Chemical Composition of Phytoplankton in Oceanic Waters," Nature, Vol. 279, 1979.

108. Parsons, P. and Masayuki, T., Biological Oceanographic Processes, Pergamon Press, Ltd., New York, 1973.

109. Denman, K., Okubo, A., and Platt, T., "The Chlorophyll Fluctuation Spectrum in the Sea," Limnology and Oceanography, Vol. 22, No. 6, p. 1033-1038, 1977.

110. Sorokin, Y.I. and Mikheev, V.N., "On Characteristics of the Peruvian Upwelling Ecosystem," Hydrobiologia, Vol. 62, No. 2, p. 165-189, 1979.

111. Shushkina, E.A. and others, "Characteristics of Functioning of Planktonic Communities in the Peruvian Upwelling," OkeanologiYa, Vol. 18, No. 5, p. 886-902, 1978.

112. Sorokin, Y., "Characteristics of Primary Production and Heterotrophic Microplankton in the Peruvian Upwelling," Okeanologiya, Vol. 18, No. 1, p. 97-110, 1978.

113. Karl, D.M., "Adenosine Triphosphate and Guanosine Triphosphate Determinations in Intertidal Sediments," In Methodology for Biomass Determinations and Microbial Activities in Sediments, ASTM STP 673, C.D. Littlefield and P.L. Seyfried, Eds., American Society for Testing and Materials, p. 5-20, 1979.

114. Karl, D.M., "Deep-Sea Primary Production at the Galapagos Hydrothermal Vents," Science, Vol. 207, p. 1345-1347.1980.

115. Karl, D.M. "Occurrence and Ecological Significance of GTP in the Ocean and in Microbial Cells," Applied and Environmental Microbiology, p. 349-355, 1978.

116. Ibid.

117. Fogg, G.E., Algal Cultures and Phytoplankton Ecology, second ed., University of Wisconsin Press, 1975.

118. Anita, N.J. and others, "Further Measurements of Primary Production in Coastal Sea Water Using a Large Volume Plastic Sphere," Limnology and Oceanography, Vol. 6, p. 237-258, 1963.

119. McAllister, C.D. and others, "Measurements of Primary Production in Coastal Sea Water Using a Large Volume Plastic Sphere," Limnology and Oceanography, Vol. 6, p. 237-258, 1961.

120. MacIsaac, J.J. and Dugdale, R.C., "Interactions of Light and Inorganic Nitrogen in Controlling Nitrogen Uptake in the Sea," Deep-Sea Research, Vol. 19, p. 209-232, 1972.

121. Caperon, J. and Meyer, J., "Nitrogen-Limited Growth of Marine Phytoplankton. I. Changes in Population Characteristics with Steady-State Growth Rate," Deep-Sea Research, Vol. 19, p. 601-618, 1972.

122. Collos, Y. and Slawyk, G., "Significance of Cellular Nitrate Content in Natural Populations of Marine Phytoplankton Growing in Shipboard Cultures," Marine Biology, Vol. 34, p. 27-32, 1976.

123. Perry, M.J., Talbot, M.C., and Alberte, R.S., "Photoadaption in Marine Phytoplankton: Response of the Photosynthetic Unit," Marine Biology (in press 1981).

124. Fogg, G.E., Algal Cultures and Phytoplankton Ecology, second ed., University of Wisconsin Press, 1975.

125. Perry, M.J. Talbot, M.C., and Alberte, R.S., "Photoadaption in Marine Phytoplankton: Response of the Photosynthetic Unit," Marine Biology (in press 1981).

126. MacIsaac, J.J. and Dugdale, R.C., "Interactions of Light and Inorganic Nitrogen in Controlling Nitrogen Uptake in the Sea," Deep-Sea Research, Vol. 19, p. 209-232, 1972.

127. Eppley, R.W., Renger, E.H., and Cullen, J.J., "Ammonium Distribution in Southern California Coastal Waters and Its Role in the Growth of Phytoplankton," Limnology and Oceanography, Vol. 24, No. 3, p. 495-509, 1979.

128. Ibid, p. 495.

129. Caperon, J. and Meyer, J., "Nitrogen-Limited Growth of Marine Phytoplankton-I. Changes in Population Characteristics with Steady-State Growth Rate," *Deep-Sea Research*, Vol. 19, p. 601-618, 1972.

130. Goldman, J.C., McCarthy, J.J., and Peavey, D.G., "Growth Rate Influence on the Chemical Composition of Phytoplankton in Oceanic Waters", *Nature*, Vol. 279, 1979.

131. Ibid

132. Ibid

133. Karl, D.M., "Occurrence and Ecological Significance of GTP in the Ocean and in Microbial Cells," *Applied and Environmental Microbiology*, p. 349-355, 1978.

134. Bronsink, S.H., *Microplanktonic ATP-Biomass and GTP-Productivity Associated with Upwelling off Pt. Sur, California,* Master's Thesis, Naval Postgraduate School, Monterey, California, 1980.

135. Karl, D.M., "Occurrence and Ecological Significance of GTP in the Ocean and in Microbial Cells," *Applied and Environmental Microbiology*, p. 349-355, 1978.

136. Costantini, R.Z. and Sturani, E., "Levels of the Ribonucleoside Triphosphates and Rate of RNA Synthesis in Neurospora Crassa," *Biochimica et Biophysica Acta*, Vol. 476, p. 272-278, 1977.

137. Holm-Hansen, O., "Carbon/ATP Ratios in Microbial Cultures and in Natural Populations," In G.A. Borun (ed.), *ATP Methodology Seminar*, SAI Technology Co., San Diego, California, p. 446-473, 1975.

138. Baugh, D.E., *RNA/DNA Ratios in the Estimation of Growth Stages of Oceanic Zooplanton Populations*, Master's Thesis, Naval Postgraduate School, Monterey, California, 1974.

139. Goldman, J.C., McCarthy, J.J., and Peavey, D.G., "Growth Rate Influence on the Chemical Composition of Phytoplankton in Oceanic Waters," *Nature*, Vol. 279, 1979.

140. Traganza, E.D., Conrad, J.W., and Breaker, L.C., "Satellite Observations of a 'Cyclonic Upwelling System' and 'Giant Plume' in the California Current," In: *Coastal Upwelling*, American Geophysical Union, Washington, D.C., 1981.

141. Eppley, R.W. and others, "A Study of Plankton Dynamics and Nutrient Cycling in the Central Gyre of the North Pacific Ocean," Limnology and Oceanography, Vol. 18, No. 4, p. 534-551, 1973.

142. Goldman, J.C., McCarthy, J.J., and Peavey, D.G., "Growth Rate Influence on the Chemical Composition of Phytoplankton in Oceanic Waters," Nature, Vol. 279, 1979.

143. Hanson, W.E., Nutrient Study of Mesoscale Thermal Features off Point Sur, California, Master's Thesis, Naval Postgraduate School, Monterey, California, 1980.

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